

A review of the genus *Mantella* (Anura, Ranidae, Mantellinae): taxonomy, distribution and conservation of Malagasy poison frogs

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In this paper, 17 species of the genus *Mantella* are recognized and the genus is partitioned into six species groups which can be distinguished by combination of bioacoustic, morphological, osteological and coloration characters. The following species and species groups are recognized: *Mantella betsileo* group (*Mantella betsileo*, *Mantella viridis*, *Mantella expectata*, *Mantella* sp. 1, and one new species described herein); *Mantella laevigata* group (*Mantella laevigata*); *Mantella cowani* group (*Mantella cowani*, *Mantella baroni*, *Mantella* aff. *baroni*, *Mantella haraldmeieri*, *Mantella nigricans*); *Mantella bernhardi* group (*Mantella bernhardi*); *Mantella madagascariensis* group (*Mantella madagascariensis*, *Mantella pulchra*); *Mantella aurantiaca* group (*Mantella aurantiaca*, *Mantella crocea*, *Mantella milotympanum*). This partition is of rather high resolution, and some of the groups may also be regarded as superspecies or species complexes.

A detailed type re-examination showed that *M. madagascariensis* and *M. baroni* represent two different species which are very similar in dorsal coloration, but *M. madagascariensis* can be distinguished by some characters of ventral coloration (horseshoe marking on the throat, reddish color ventrally on femur) and morphology (large inner metatarsal tubercle) from *M. baroni*.

Specimens from Marojezy preserved in the Paris museum are catalogued as *M. cowani nigricans* and must therefore be considered as syntypes of this taxon. The syntype series is heterogeneous, also containing specimens of *M. laevigata*. The name *nigricans* is stabilized by designation of a lectotype corresponding to a *M. cowani* group form from Marojezy. The name *Mantella cowani nigricans* Guibé, 1978 is revalidated and raised to species rank as *Mantella nigricans*.

A big problem in *Mantella* systematics is that, in recent years, hobbyists increasingly tend to publish "phantom" scientific names without type designation which in several cases lead to involuntary but nomenclaturally available new nominal taxa. Two phantom names which must be considered as nomenclaturally available are *Mantella aurantiaca milotympanum* Staniszewski, 1996 and *Mantella aurantiaca rubra* Staniszewski, 1996. We consider the name *rubra* as synonym of *M. aurantiaca*, but preliminarily attribute specific status to *M. milotympanum*.

Lectotypes (in addition to *M. nigricans*) are designated for *M. cowani*, *M. aurantiaca*, *M. betsileo*, *Mantella attemsi* (synonym of *M. betsileo*), *M. aurantiaca rubra* (synonym of *M. aurantiaca*) and *M. milotympanum*.

(from published figure). Clarifications on types and type series are provided for several species.

We provide a key to the species of the genus *Mantella*, and describe and discuss their color variability. In several species, a large intraspecific color variability was recorded (*M. aff. baroni*, *M. nigricans*, *M. crocea*). A detailed review of all published *Mantella* localities and the corresponding voucher specimens results in updated distribution maps. Sympatric and syntopic occurrence was reliably only found in species from different species groups, the species within each group being allopatrically distributed. Future studies on contact and hybrid zones may demonstrate that some of the species recognized herein should possibly better be regarded as subspecies; however, for practical reasons, we here regard all taxa as species.

In an attempt to provide an estimate of the conservation status of each *Mantella* species, we combined data on distribution (maximum locality distance, number of known localities), habitat (primary forest restriction), trade intensity and attractiveness to the pet trade. We group the species in various classes, according to their potential vulnerability, and outline priorities of research needed to get a more reliable data basis for such estimates.

INTRODUCTION

The ranoid subfamily Mantellinae currently contains two genera, both endemic to Madagascar (GLAW & VENCES, 1994): the type genus *Mantella*, and the large and heterogeneous *Mantidactylus* with currently 63 species. *Mantella* are small, largely diurnal and often colorful frogs, which were named Malagasy (or Madagascan) poison frogs due to the presence of alkaloid toxins in their skin (e.g. DALY et al., 1996).

Accounts on the genus were published by GUIBÉ (1964, 1978) and BUSSE (1981). BLOMMERS-SCHLÖSSER & BLANC (1991) largely relied on BUSSE's revision which they complemented by detailed distribution maps. The description of four new species by PINTAK & BÖHME (1988, 1990), BUSSE & BÖHME (1992) and VENCES et al. (1994) demonstrated, however, that those accounts were far from being complete. While GUIBÉ (1978) listed only four species and one subspecies, GLAW & VENCES (1994) already accepted 13 different species.

One of the major problems in *Mantella* systematics has been weak morphological differentiation. Since early workers generally studied only preserved material, they had to rely largely on color pattern for species diagnoses. GUIBÉ (1964, 1978) and especially BUSSE (1981) considered single species (named *M. cowani* or *M. madagascariensis*, respectively) as highly variable in coloration, but they never proved this variability in specimens from a single locality (DALY et al., 1996). Without definite knowledge of intra- and interpopulational color variability, the attribution of type specimens of early names (*M. madagascariensis*, *M. cowani*, *M. baroni*, *M. pulchra*) largely depended on the subjective impression of the corresponding author, causing large confusion in the usage of these names in scientific and non-scientific literature.

In the following we report the main results on taxonomy, distribution and color variability of *Mantella* which were gathered in the framework of a comprehensive study of the genus. Contributions to the morphometry, osteology, tadpole morphology, reproduction, karyology, as well as bioacoustic and allozyme differentiation within *Mantella* are being published elsewhere. The aim of the present paper is mainly to clarify the taxonomy and nomenclature

of *Mantella* species as well as their distribution, in order to give a more stable basis for future investigations of these frogs. We divide the genus into phenetic species groups, and use our new scheme of *Mantella* systematics to discuss biogeographical subjects and to summarize conservation needs.

MATERIAL AND METHODS

SPECIMENS EXAMINED

The present review is mainly based on preserved material of the following collections: The Natural History Museum, London (BMNH); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Museo Regionale di Scienze Naturali, Torino (MRSN/MZUT); Naturhistorisches Museum Basel (NMB); Naturhistorisches Museum Wien (NMW); Transvaal Museum, Pretoria (TM); Zoologisch Museum Amsterdam (ZMA); Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). Specimens were examined in detail and their color patterns and morphology recorded. Locality and collector are generally literally given according to the corresponding catalogue. Abbreviations used are: CS, cleared and stained specimens; TE, tissue extracted for electrophoresis, specimens only partly preserved (generally liver extracted and two limbs amputated); NIL, specimens not individually labeled. The term "ex" is used in the sense of "formerly" to characterize old collection numbers.

LOCALITIES AND DISTRIBUTION MAPS

The examined material is the basis of the locality maps and the statements on color variability. Localities are numbered, the numbers corresponding to those in the respective distribution maps. A star behind the locality number marks the localities which were confirmed by FG (and partly by MV) in the field. The type locality, in the nomenclatural account on each taxon, is given in quotation marks literally as in the original description; additional discussions, when necessary, are provided in the *Comments* sections.

DESCRIPTION OF COLOR PATTERNS

Variation of color patterns is described in a standardized way and generally refers to live coloration of adult specimens. Terms which we use to refer to certain color elements are defined as follows: (1) dorsolateral color border: a sharp longitudinal border between the color of the flanks (darker) and the dorsum (lighter); (2) frenal stripe: a light longitudinal stripe along the upper lip; (3) rostral stripe: a light (yellowish, greenish or brownish) stripe running from anterior head tip and nostril above the eye to a point behind the eye;

(4) diamond marking: a central (dark) marking on the back of more or less distinct double-rhomboid shape; (5) flank blotches: light markings of varying extension which are located posterodorsally around the forelimb insertion and anterodorsally around the hindlimb insertion; they mostly can be seen as an extension of the dorsal humerus/femur color on the flanks; (6) flashmark: a sharply delimited, bright orange or red marking on the posterodorsal femur, knee hollow and ventral tibia which in some species can cover the ventral tibia nearly entirely; (7) horseshoe marking: a light (generally whitish blue) continuous marking on the throat, running more or less broadly along the lower lip and thus horseshoe-shaped. The terms femur, tibia, and tarsus, as used in the sections on coloration, do not refer to the skeletal elements but to the external coloration of the corresponding hindlimb sections.

MORPHOMETRY AND MORPHOLOGY

Measurements taken were: SVL: snout-vent length; HW: maximum head width; HL: head length, measured from snout tip to forelimb insertion (not to maxilla articulation); Eye: horizontal eye diameter; Tym: horizontal tympanum diameter; Eye-Ns: distance between eye and nostril; Ns-St: distance between nostril and snout tip; ForL: forelimb length; HaL: hand length; HiL: hindlimb length; FoTL: foot length including tarsus; FoL: foot length; ToL1: length of first toe; FW3: width of third finger just before terminal finger disk; DW3: width of terminal disk of third finger; IMTL, IMTH, IMTW: length, height and width of inner metatarsal tubercle. All measurements were made by the senior author with a precision calliper to the nearest 0.1 mm, except FW3, DW3, IMTL, IMTH, IMTW which were measured using a binocular with measuring device to the nearest 0.01 mm or, when no binocular was available, with a calliper to the nearest 0.1 mm. Original measurements in the present paper are only given for type specimens, but the size ranges and morphometric ratios in the species accounts refer to a total of about 400 measured specimens.

In the text, besides SVL, we use the abbreviations IMT for inner metatarsal tubercle, and TTA for tibiotarsal articulation. The size (SVL) is given as range of adult specimens, followed where possible by the range recorded in the males and females which could be reliably sexed. Since in many cases specimens could not be sexed with a sufficient reliability, known adult size range may be wider than that recorded in males and females separately.

DESCRIPTION OF CALLS

Detailed call descriptions will be published elsewhere; here we tentatively distinguish four different general call types: (1) double click calls are series of notes which each are composed of two emphasized and very short "metallic" clicks; (2) single click calls are series of notes which each are composed of one emphasized and very short "metallic" click; (3) trill calls are (irregularly repeated) notes composed of up to 10 short clicks; (4) chirp calls consist of (irregularly or regularly repeated) notes with a less "metallic" appearance than in click calls as used above (a note is often composed of 2-3 emphasized pulses).

SYNONYMIES

For each *Mantella* species, we present a synonymy and chresonymy (for the definition of the term chresonymy, see SMITH & SMITH, 1973), following the scheme used by DAVID & VOGEL (1996). The overwhelming number of publications in which at least one species of *Mantella* is mentioned makes it impossible to provide a complete chresonymy. Instead, we present a selection of references (partial chresonymy) which either (1) discuss intrageneric taxonomy and systematics, (2) provide original data for at least one species, (3) include pictures of at least one species, or (4) were published before GUIBÉ's (1964) revision of the genus (the latter, however, must be seen with reservation since it is often difficult to understand to which species the author actually referred). Page numbers are only given if necessary to locate a deviating name usage or a figure. Only publications which contain either original data or figures are listed in the chresonymies of the species. Exceptions are the works of GUIBÉ (1964, 1978), BUSSE (1981), BLOMMERS-SCHLÖSSER & BLANC (1991) and GLAW & VENCES (1992a, 1994), which are here considered as monographic accounts on the genus. All names used in these works are listed in the corresponding synonymies. Generally, taxa which were defined in a publication in a way that, according to present definition, they were in fact composed of several species, are listed as "partim-chresonyms" ("part.") in the chresonymies of each of these species (in the case of monographs) or of the species which were shown or explicitly meant (in the case of other papers). Nomenclatural validity of names is discussed according to the *International Code of Zoological Nomenclature* (ANONYMOUS, 1985; cited below as "the Code").

RESULTS

THE GENUS *MANTELLA**Definition of the genus*

Following the data of GUIBÉ (1978), BLOMMERS-SCHLÖSSER & BLANC (1991), BLOMMERS-SCHLÖSSER (1993), DALY et al. (1996), GLAW et al. (1998b), PINTAK et al. (1998), VENCES & KNIEL (1998) and VENCES et al. (1998, 1999a), the genus *Mantella* can be defined by the combination of the following characters:

(1) Eight presacral vertebrae; (2) vertebral centrae procoelous; (3) sacral diapophyses not enlarged; (4) atlantal cotyles widely separated; (5) three free distal tarsals; (6) six free distal carpals; (7) terminal phalanges slightly Y-shaped; (8) hyoid with anterolateral and posterolateral processes; (9) anterior processes of hyalia forming complete arch in some specimens of most or all species; (10) palatines present; (11) maxillary and premaxillary teeth absent; (12) vomer present; (13) dentigerous process of vomer (and thus vomerine teeth) absent; (14) squamosal with reduced zygomatic process; (15) frontoparietals anteriorly convex-shaped and separated along their whole length; (16) process of pars fascialis of maxilla reduced; (17) shoulder girdle firmisternal; (18) ossified sternum and omosternum present; (19) sternum

shorter than omosternum; (20) omosternum forked at its base; (21) complete ventral circum-marginal groove on terminal finger and toe expansions; (22) SVL of adults 18-31 mm; (23) tibiotarsal articulation reaching between forelimb insertion and nostril; (24) tympanum visible externally, mean tympanum/eye ratio 1/2 to 2/3; (25) lateral metatarsalia connected; (26) no webbing between fingers nor toes; (27) inner and outer metatarsal tubercle present; (28) no dorsal "scutes" on finger and toe tips; (29) karyotype $2n = 26$, with 5 pairs of large and 8 pairs of small chromosomes which are meta- or submetacentric; (30) tongue very slightly notched; (31) microphagous and myrmecophagous feeding; (32) skin alkaloids present; (33) long prey-capture jumps absent; (34) colorful pattern at least ventrally (black/blue, yellow or orange), often also dorsally; (35) activity largely diurnal; (36) calls consisting of short clicks, chirps or trills; (37) no strong mating amplexus; (38) eggs generally laid outside of the water; (39) eggs unpigmented; (40) tadpoles with horny beak and keratodont formula 1:2+2/3 to 1:5+5/3 (formula according to DUBOIS, 1995); (41) no tadpole transport; (42) no external gills in early larval stages; (43) egg clutches consisting of less than 200 eggs; (44) no externally prominent femoral glands as in many *Mantidactylus*, but granular thigh patches present (see also DALY et al., 1996), most distinct in males (exact structure of these patches will be subject to a forthcoming publication).

Character states 9, 11, 14, 30, 31, 32, 33 and 34 are, as far as known, not found in *Mantidactylus*, the second genus of the Mantellinae. They all can be considered as derived in *Mantella* (based on outgroup comparison with other ranid frogs, e.g. the Malagasy rhacophorines of the genus *Boophis*). However, states of characters 11, 13, 14, 16, 30, 32, 33, 34 and 35 are all part of a character complex related to microphagy (character 31), which reduces their value as independent characters for the assessment of phylogenetic relationships (see VENCES et al., 1998). In fact, most of them are also found in the Dendrobatidae which, too, are microphagous but clearly differ from *Mantella* in other characters (different states in characters 5, 6, 7, 18, 20, 28, 29, 30, 40, 41 and 42; for references, see VENCES et al., 1998). Apomorphic states supporting the status of *Mantella* as a monophyletic (holophyletic) group within the Mantellinae are thus the microphagy character complex (see above) and the hyoid structure (character 9).

Etymology of the generic name

The genus *Mantella* was erected by BOULENGER (1882) to accommodate the species *betsileo*, *madagascariensis* and *ebenau*; in an addendum he described the new species *cowanii*. The type species is *Mantella betsileo*, as designated by LIEM (1970). No etymology was given in the original description of the genus. The generic name is most probably a diminutive of *mantis* (Classical Greek *mantis*, prophet) which was used with the meaning "treefrog" in the sense of a weather prophet by HESYCHIOS. This meaning of *mantis* is included in several Greek-German dictionaries (e.g. PAPE, 1888) but was not found in Greek-French or Greek-English dictionaries (see GLAW & VENCES, 1994: 400). The term *mantis* was often used for generic anuran names; BOULENGER himself erected in 1895 the genus *Mantidactylus* for several Madagascan frogs which today are included together with *Mantella* in the Mantellinae.

A second etymology for *Mantella*, however, cannot be totally excluded. One of the early subjects of BOULENGER's studies were dinosaur fossils found in Belgium, which belonged to the genus *Iguanodon*. The first *Iguanodon* fossils had been found by an English doctor,

G MANTPELL, and his wife, and were subsequently described as *Iguanodon mantelli* (see BULTYNCK, 1987). Still less probable is a derivation from the Italian word *mantella* (cloak) which is sometimes used to describe animal (mammal) color patterns.

DEFINITION OF SPECIES GROUPS

Although several authors have stressed similarities between selected *Mantella* species and erected species groups within the genus (GLAW & VENCES, 1994, ZIMMERMANN, 1996a; STANISZEWSKI, 1996), no comprehensive attempt has so far been published to partition the whole genus into such groups, and to explicitly list the characters distinguishing them. We here divide the genus into six phenetic species groups, a subdivision of rather high resolution; in fact, some groups could also be characterized as superspecies or species complexes. The differential characters between species groups are summarized in tab. 1.

Mantella betsileo group (contains: *Mantella betsileo*, *M* sp. 1, *M. viridis*, *M. expectata*, and one new species described herein). – This group is characterized by the combination of several characters which, however, are each also present in at least one other species group: double click call (also in *M. laevigata*), horseshoe marking (also in several other groups), frenal stripe (also in *M. crocea* and some *M. madagascariensis*), hindlimbs ventrally black without orange and red (also in *M. laevigata* and *M. nigricans*).

Mantella laevigata group (contains: *Mantella laevigata*). – The classification of *Mantella laevigata* in a separate species group is clearly justified by its unique habits (partly arboreal, tree hole breeding, single eggs) and its distinctly enlarged finger tips. It is the only species with a double click call which lacks a horseshoe marking.

Mantella cowani group (contains: *Mantella baroni*, *M. aff. baroni*, *M. cowani*, *M. nigricans*, *M. haraldmeieri*). A group characterized by light (mostly yellow or red) flank blotches of variable extension (also found in the *M. madagascariensis* group and in *M. bernhardi*) and single click calls (exclusive to this group).

Mantella bernhardi group (contains: *Mantella bernhardi*). Classification of *M. bernhardi* in a separate species group is mainly based on its relevant allozyme differentiation (VENCES et al., 1999b) and its trill calls.

Mantella madagascariensis group (contains: *Mantella madagascariensis*, *M. pulchra*). – The species included in this group are mainly characterized by a very large IMT (see diagnosis of *M. pulchra* in GÜNTHER, 1964, 1978). Light flank blotches of varying extension, horseshoe markings and flashmarks are present. Calls, as far as known, are chirp calls.

Mantella aurantiaca group (contains: *Mantella aurantiaca*, *M. crocea*, *M. milotympanum*). – Species of this group are characterized by a rather stout body shape, distinct flashmarks and a chirp call. In contrast to species of the *M. madagascariensis* group, there are no flank blotches and the IMT is smaller. Two species (*M. aurantiaca*, *M. milotympanum*) are characterized by a largely uniform yellow to red dorsal and ventral coloration. *M. crocea* is included in this group since specimens with color pattern intermediate between *M. crocea* and *M. milotympanum* are known (GLAW & VENCES, 1998), and juvenile coloration of *M. crocea* and *M. aurantiaca* is very similar (personal observation). The close relationships between the

Table 1 Differential characters between *Mantella* species groups. Not all characters have been ascertained in all species of the groups. See *Definition of species groups* section for more information. Sternum shape is given according to VENCES et al. (1999a). IMT, inner metatarsal tubercle.

Character	<i>Mantella betsileo</i> group	<i>Mantella laevigata</i> group	<i>Mantella cowani</i> group	<i>Mantella bernhardi</i> group	<i>Mantella madagascariensis</i> group	<i>Mantella aurantiaca</i> group
Call	mostly double click, series	double click, series	single click, series	trill, mostly no series	chirp, series	chirp, mostly no series ¹
Sternum	forked	forked	unforked	unforked	forked	forked
Horseshoe marking	present	absent	absent	present	present	present/absent
Frenal stripe	present	absent	absent	absent	absent (present) ²	present/absent
Flank blotches	absent	absent	large/small	small	large	absent
Orange/red ventral color on hindlimbs	absent	absent	present (absent) ³	present	present	present
Habitat	terrestrial	partly arboreal	terrestrial	terrestrial	terrestrial	terrestrial
Eggs laid as	clumps	single eggs	clumps	clumps	clumps	clumps
Egg feeding of tadpoles	absent	present	absent	absent	absent	absent
IMT	small	small	small	small	large	small

Only ascertained in *M. aurantiaca*, *M. crocea* calls are also chirp calls (personal observation), but notes may be arranged more often in series than in *M. aurantiaca*.

² A frenal stripe may be present in certain specimens of the "variable" morph of *M. madagascariensis*.

³ Orange/red ventral color on hindlimbs is present in all species of the *M. cowani* group except *M. nigricans*.

species of the *M. aurantiaca* group were supported by chromosome morphology (PINTAK et al., 1998) and by studies on allozyme variation (VENCES et al., 1999b). ZIMMERMANN (1996) also mentioned a *M. aurantiaca* group which included *M. aurantiaca* and *M. crocea*.

SPECIES ACCOUNTS

In the following, we list *Mantella* species separately for each species group; within the groups, species are arranged alphabetically. Photographs of living specimens of all species are shown in fig. 1-3, dorsal and ventral views of holotypes and lectotypes (all photographed 1992-1999) in fig. 4-5, and variation of ventral pattern in fig. 6-8. Distribution maps are shown in fig. 9.

Mantella betsileo group

Mantella betsileo (Grandidier, 1872)

Dendrobates betsileo Grandidier, 1872. Name-bearing type lectotype, by present designation MNHN 1895 278, sex unknown due to bad state of preservation, SVL 19.0 mm. *Type locality* "Pays des Betsileos" according to original description and MNHN catalogue. *Other types* paralectotype, following present lectotype designation, MNHN 1895 279. - *Etymology* named after the type locality, the region Betsileo.

Mantella betsileo BOULENGER, 1882, 1888, VAILLANT, 1885, WERNER, 1901, MOCOQUARD, 1909, METHUEN & HEWITT, 1913, MILLOT & GUILBE, 1951, GUILBE, 1964, 1978, LIEM, 1970, BACHMANN & BLOMMERS-SCHLOSSER, 1975, BLOMMERS-SCHLOSSER, 1978, 1979a, MEIER, 1980 (part, p. 353, third figure from above), 1986 (Abb. 3); BUSSE, 1981 (part.; see *M. haraldmeieri*); PINTAK, 1990, BLOMMERS-SCHLOSSER & BLANC, 1991 (part.), 1993 (plate 19 101), ANDREONE, 1992 (pl. III fig. 3-4), GLAW & VENCES, 1992a (part., see localities) 1992b (fig. p. 29), 1994 (part., see localities), ZIMMERMANN & ZIMMERMANN, 1997 (fig. 5 17) GARRAFFO et al., 1993, HERRMANN, 1993 (fig.), KUXHLING, 1993; BARTLETT, 1995 (fig. p. 26), HENKEL & SCHMIDT, 1995 (fig. p. 50); CARISSIMI-PRIORI, 1995 (fig. p. 42); VENCES et al., 1996, 1998, DALY et al., 1996; STANISZEWSKI, 1997a (fig.), 1997b (fig.); LARSEN, 1997; PINTAK et al., 1998, VENCES & KNIEL, 1998

Dendrobates ebenau Boettger, 1880. Name-bearing type lectotype, by designation of MERTENS (1967: 44), SMF 7323 (ex 1141, 1a), adult female. - *Type locality* "insula Nossi Be", according to original description. *Other types* possibly one paralectotype, FMNH 18236 or 18237 (see MARX, 1958, and comment below). - *Etymology* named after C. EBENAU who provided the type material.

Dendrobates Ebenau MOCOQUARD, 1909 (syn. *betsileo*), MERTENS, 1922 (syn. *betsileo*), MERTENS, 1967 (syn. *betsileo*)

Dendrobates ebenau GUILBE, 1964 1978 (syn. *betsileo*), BUSSE, 1981 (syn. *betsileo*), BLOMMERS-SCHLOSSER & BLANC, 1991 (syn. *betsileo*), GLAW & VENCES, 1994 (syn. *betsileo*; p. 411)

Mantella ebenau BOULENGER, 1882, WERNER, 1901, METHUEN & HEWITT, 1913 (syn. *betsileo*)

Mantella attemsi Werner, 1901. Name-bearing type lectotype, by present designation, NMW 20837, female, SVL 25.6 mm. *Type locality* uncertain, but (in original description) was speculated to be probably Madagascar oder Nossi-Be. *Other types* paralectotype, following present lectotype designation, ZMB 16588. *Etymology* named after C. ATTEMIS who provided the type specimens from Zanzibar.

Mantella Attemsi MOCOQUARD, 1909

Mantella attemsi GUILBE, 1964, 1978 (syn. *betsileo*), BUSSE, 1981 (syn. *betsileo*), BLOMMERS-SCHLOSSER & BLANC, 1991 (syn. *betsileo*), GLAW & VENCES, 1994 (syn. *betsileo*; p. 412); HAUPI et al., 1994 (syn. *betsileo*)

Identity DALY et al. (1996) were concerned about the fact that the type locality of *M. betsileo* (see below) is outside the known range of the species. They questioned whether the name is currently correctly applied. A re-examination of the types (see below) leads us to

conclude that they (1) cannot be conspecific with any species having red or orange ventral color on the hindlimbs, (2) are morphologically different from *M. laevigata* and *M. nigricans*, and (3) are smaller than *M. viridis*, *M. sp. 1* and *M. expectata*. It seems therefore likely that the name is currently (e.g. GLAW & VENCES, 1994) correctly applied.

Comments. - (1) The taxon *betsileo* was originally based on the syntypes MNHN 1895.278-279. The lectotype MNHN 1895.278 (SVL 19.0 mm; sex unknown) is larger and in slightly better state of preservation. The paralectotype MNHN 1895.279 is probably a subadult specimen (SVL 15.7 mm). In both types, coloration has become a contrastless, nearly uniform brown. The dorsolateral coloration border mentioned in the original description cannot be unequivocally recognized. Since the hindlimbs were folded in both specimens, the pattern is less faded on the posteriorly directed (ventral) part of the tibia which was not exposed to light. Here, a distinct light crossband can be recognized, as is typical for species of the *M. betsileo* group (and for *M. laevigata* and *M. nigricans*). Based on this character it can be excluded that the types are conspecific with *Mantella* species having red or orange color ventrally on the hindlimbs. (2) The type locality of *M. betsileo* is a large region in central Madagascar. Up to now, no *Mantella betsileo* specimens are known to have been collected in the eastern forests south of Nosy Boraha. As discussed by DALY et al. (1996), the travel routes of GRANDIDIER are rather well documented. Maybe, the types were not collected in the eastern Betsileo forests but in western Betsileo, where the occurrence of *M. betsileo* seems more probable due to the existence of several localities in western Madagascar. It also cannot be excluded that the type locality is wrong. (3) According to the original description (BOETTGER, 1880: 281), *Dendrobates ebenaui* was based on two syntypes, a male and a female. However, in his 1892 catalogue, BOETTGER (1892: 21) mentioned "numerous specimens" ("Zahlr. Stk") of this species from Nossibé, kept in the Frankfurt Museum under number SMF 1141.1a; presumably these specimens included the two original syntypes and several other non-type specimens. MERTENS (1922: 166) stated that the "Typus" of this species was bearing the number SMF 1141.1a, but since this number was used by BOETTGER (1892) as a collective number for a series, this mention cannot be considered as a lectotype designation under article 47 (b) of the Code. Designation of an individual specimen, SMF 7323, as lectotype of this species, was made by MERTENS (1967: 44). Thus, only one paralectotype exists. It might be one of the two FMNH "paratypes" listed by MARX (1958), which were presumably part of the series mentioned by BOETTGER (1892). Further clarification of the status of these two specimens is necessary. (4) The description of *Mantella attemsi* was based on two specimens (WERNER, 1901), corresponding to the specimens NMW 20837 and ZMB 16588. Both are today in a rather bad state of preservation. Color patterns are largely faded, only the dorsolateral color border is still recognizable. In the lectotype NMW 20837, a few ventral color patterns (light vermiculated markings on the posterior venter) are still faintly recognizable. The paralectotype ZMB 16588 is most probably a male.

Material examined. - Difficulty of identification of specimens as *M. betsileo* is enhanced by the existence of a very similar, undescribed species (*M. sp. 1*, see below). Since this species is generally larger than *M. betsileo*, size was one of the major diagnostic characters for preserved specimens with faded coloration. However, we cannot totally exclude that some specimens may be wrongly identified and in fact be subadults of *M. sp. 1*. In parentheses, we give SVL for most specimens.

The following specimens can clearly be assigned to *M. betsileo*: BMNH 84.11.3.4 (Nosy Be, purch from "Linnaea"), BMNH 86.2.25.25-28 (Nosy Be, "Senckenberg Museum"; NL, SVL 23.7 mm.

20.7 mm, 22.2 mm, 23.3 mm), BMNH 1909 10 19 21 (Nosy Be; P. KREFFT), BMNH 1926 10 27 4-7 (Antongil forest, Maroantsetra, purch. ROSENBERG; NIL; largest female 25.3 mm); BMNH 1952 1.1.55-56 (Rantabe, Antongil bay, Maroantsetra; coll. C. S. WEBB, female 55.25.7 mm); ZFMK 17604-9 (Maroantsetra; leg. H. MELIER I 1976); ZFMK 27680 (Maroantsetra, leg. H. MELIER X 1979); ZFMK 28867-8 (Nossi-Bé; through Linnaea 1886, originally Museum Göttingen), ZFMK 46004 (Nosy Boraha [Ile Ste Marie], leg. F. W. HFNKEL II.1987 CS); ZFMK 46781-3 (Nosy Be Loucoube, leg. R. SEIPP IV 1987), ZFMK 47007 (Nosy Bé Loucoubé, leg. F. W. HFNKEL & J. SAMEIT II 1987), ZFMK 47218 (Sahafary, leg. F. GLAW XI 1987), ZFMK 47289 (Nosy Boraha [Ile Ste Marie], leg. H. MELIER XI 1987), ZFMK 48257-8 (Nosy Bé Loucoubé, leg. W. SCHMIDT 1987), ZFMK 52744 (Nosy Boraha [Ile Ste Marie], leg. F. GLAW & M. VENCES III 1991); ZFMK 52745 (Nosy Be, leg. F. GLAW & M. VENCES III 1991), ZFMK 51818 (Nosy Boraha [Ile Ste Marie], leg. F. W. HFNKEL et al. 1988 89), ZFMK 53708-10 (Nosy Be, leg. F. GLAW & J. MULLER II 1992, juveniles), ZFMK 59978-9 (Kirindy, leg. F. GLAW I 1995), ZFMK 62685-7 (locality unknown, CS), ZFMK 62689-96 (locality unknown, TE); ZFMK 62688 (Nosy Be, leg. K. SCHMIDT, TE), MRSN A0064 1-4 (Maroantsetra, leg. F. ANDRLOM 23 IV 1990); MRSN A0068.1-2 (Kirindy, leg. R. NINCHERI 22 XII 1992).

The following specimens are assigned to *M. betsileo* based on size, general appearance and morphometric characters such as relative hindlimb length. BMNH 94 2 27.21 (Madagascar, coll. LAST, purch. GERARD, pattern totally faded), BMNH 1930 7 1 54-57 (valley 3/4 miles W of Ampoza, 15 miles E of Ankazoabo, SW Madagascar, pres. WHITE; rather small specimens, NIL), MNHN 1884 603-4 (Nossi-Bé, SVL 25 mm [603], 21 mm [604]), MNHN 1885 34-7 (locality unknown, SVL 21 mm [34], 18 mm [35], 20 mm [36], 18 mm [37]), MNHN 1885 48 (Nossi-Bé), MNHN 1895 278 9 (lectotype and paratype, Pays des Betsileos), MNHN 1896 435-6 (Madagascar, "acquis de l'Institut Linnaea", color totally faded, SVL 24 mm [435, female?], 23 mm [436]), MNHN 1900 15 (Pays Mahafaly, au Sud, with remark "mâle Joly", SVL 20 mm), MNHN 1929 225 (source de Namoroko [Ambongo], juv. ♀, SVL 16 mm), MNHN 1953 129, MNHN 1991 1795 [originally 129a] (forêt d'Antyaba; TTA reaches eye center [1795], SVL 25 mm [129], 24 mm [1795], few ventral markings, absent on breast [1795]), MNHN 1953 131, MNHN 1991 1796 [originally 131a] (Bas Manongarivo, SVL 17 mm [131], 16 mm [1796]), MNHN 1953 130, MNHN 1953 133 (locality unknown, SVL 23 mm [130, 133]), MNHN 1953 134 (Nossi-Bé Lokobe, Manjoky, juv., SVL 13 mm), MNHN 1962 895 (Namoroka, grotte de Bemahara, R. PAULIAN IX 52, TTA reaches eye center, SVL 27 mm), MNHN 1962 896-7 (Anove, forêt littorale, A. DOMINGUE I 1961, TTA reaches eye center [896, 897], SVL 21 mm [896], 22 mm [897]), MNHN 1976 200-2 (Nosy Komba, SVL 21.1 mm [200], 19.7 mm [201], 19.3 mm [203]), TM 9858-67 (Eastern Region, Madagascar, coll. HIRSCHHELL-CHAUVIN).

The following MNHN specimens with unknown locality are here assigned to *M. betsileo* only based on their size which is given in parentheses. MNHN 1976 181 2 (SVL 22.3 mm [181], 22.0 mm [182]), MNHN 1976 187 (SVL 22.2 mm), MNHN 1976 206 (SVL 19.5 mm), MNHN 1976 222-3 (SVL 20.9 mm [222], 17.6 mm [223]), MNHN 1976 225 (SVL 22.1 mm), MNHN 1976 227 (SVL 22.1 mm), MNHN 1976 230 (SVL 22.8 mm).

The status of two specimens is not sufficiently clarified. They have enlarged disks on fingers and toes and thus resemble *M. laevigata*. MNHN 1953 132, MNHN 1991 1797 [originally 132a] (Isaratanana, TTA reaches between tympanum and eye [132], SVL 25 mm [132], 20.5 mm [1797]).

Distribution—Except the type locality "Pays des Betsileos", all known localities are located in lowlands (altitude between 0 and ca. 500 m), generally near the coast. Also, all east coast localities are in an area north of Betsileo (see DALY et al., 1996: 19). Confirmation of the type locality would therefore be important.

The species is common along the east coast in the Maroantsetra region and on Nosy Boraha, and in the Sambirano region, it also occurs along the west coast. Localities are as follows: [1*] Nosy Boraha (<10 m altitude); [2*] Voloina (GLAW & VENCES, observations in 1991), [3] Maroantsetra, [4] Rantabe, [5*] Sahafary; [6] Anove, [7] Antanambaobe, and Ambavala near Sanjakatsy in the Mananara reserve (DALY et al., 1996, 100-200 m altitude); [8] Farakarina near Maroantsetra (DALY et al., 1996, 30 m altitude), [9*] Nosy Be, [10*]

Nosy Komba; [11*] Benavony (F. GLAW & J. MÜLLER, observations in 1992); [12] Ankify (village near ferry docks N Ambanja, personal communication of W. B. LOVE); [13] Manongarivo; [14] Tsaratanana (SCHIMMENTI, personal communication); [15*] Kirindy (Amborom-potsy, see KUCHLING, 1993); [16] Namoroka, [17] Tsingy de Bemaraha (SCHIMMENTI, personal communication); [18] Mahafaly (?); [19] Ampoza (not traced and therefore not included in the distribution map).

The Mahafaly locality (MNHN 1900 15) in the very arid South-Western Region needs confirmation but seems corroborated by the specimens from Ampoza in SW-Madagascar, and is therefore accepted here in a preliminary way. Specimens from the Anosy mountains in southern Madagascar identified as *M. betsileo* by BUSSE (1981) in fact belong to *M. haraldmeieri* (see below). MILLOT & GUIBÉ (1951) mentioned the species from the "forêt de Bevia" near Fort Dauphin, but we could not find voucher specimens for this locality in the Paris Museum. Also HENKFL & SCHMIDT (1995) gave no vouchers for their locality Tolagnaro. We consider these localities in need of confirmation, and do not accept them here.

We did not find voucher specimens for seven additional localities which were listed by BLOMMERS-SCHLÖSSER & BLANC (1991). Of these, Nosy Mangabe probably was based on BUSSE (1981: 29) who stated that specimens of *M. laevigata* collected by H. MEIER (on Nosy Mangabe) lived parapatrically or sympatrically with *M. betsileo*. We did not find *M. betsileo* on Nosy Mangabe, and the locality thus needs confirmation. The population from Montagne des Français (near Antsiranana) is here referred to *M. viridis* (see below), and those from Morondava, Androatsabo and Tongahybe to *M. sp. 1* (see below). Baly probably refers to Tongahybe, since in the Paris Museum catalogue the additional remark "Baly Ouest" is given for the corresponding specimens (see section on *M. sp. 1*). We did not find vouchers from Andranoboka in the Paris Museum and therefore consider this locality in need of confirmation.

Diagnosis (1) *Morphology* A small, relatively slender *Mantella*. SVL, males 18-21 mm, females 19-26 mm. TTA mostly reaching eye center. Terminal disks of fingers and toes expanded. Tympanum/eye ratio generally 1/2 to 3/5. IMT medium sized (ratio width/length about 2/3). (2) *Dorsal color and pattern*. Dorsal head surface and dorsum yellowish to orange or light brown, mostly with a diamond marking and a sharp dorsolateral color border to the largely black flanks. White frenal stripe present. Limbs brown to grey, with at least one dark brown crossband on femur, tibia and tarsus. Iris with light pigment in its upper part. (3) *Ventral color and pattern* Black with blue markings of different size and extension often showing vermiculated patterns and fusing with each other. Breast region generally with light markings, smaller than those on posterior venter. Distinct horseshoe marking present, of larger extension in males than in females, and sometimes including a central stripe.

***Mantella expectata* Busse & Bohme, 1992**

Mantella expectata Busse & Bohme, 1992. *Name-bearing type* holotype by original designation (BUSSE & BOHME 1992: 58), ZFMK 53540 male, SVL 23.4 mm. *Type locality* "20 km southeast of Tolara I (=Tulear), W-Madagascar" according to original description. *Other types* paratypes ZFMK 53541-2, ZFMK 59095 8 and four (lost) additional paratypes (see comment below). *Etymology* derived from Latin *expectare* (to await), rediscovery of this species was awaited during several years after MEIER (1986) first published a picture of it.

Mantella expectata GLAW & VENCES, 1992a, 1994, HERRMANN, 1993 (fig.), LE BERRÉ, 1993 (fig. p. 20), HENKEL & SCHMIDT, 1995 (fig. p. 52), BARTLETT, 1995 (fig. p. 26), VENCES et al., 1996, DALY et al., 1996, STANISZEWSKI, 1996 (plate p. 18), 1997a (fig. p. 16), 1997b (fig.), 1998a (fig.); VENCES & KNIEL, 1998

Other chresonyms:

Pictured in MEIER (1986 fig. 8) as "Eine noch unbekannte *Mantella*-Form".

Comment In the original description (BUSSE & BÖHME, 1992), beside the catalogued specimens ZFMK 53541-2, "eight living specimens which will be incorporated in the ZFMK collection later" were also designated as paratypes. Of these captive stock, only four specimens were eventually preserved and catalogued as ZFMK 59095-8; the remaining four paratypes must be considered as lost

Material examined ZFMK 53540 (SE Tulear, leg. G. GOTTLIEB II 1992, holotype); ZFMK 53541-2 (SE Tulear, leg. G. GOTTLIEB II 1992, paratypes), ZFMK 59095-8 (SE Tulear, through pet trade, paratypes), ZFMK 62713-5, ZFMK 62789 (locality unknown; TE), ZFMK 62716-7 (locality unknown, CS)

Distribution – Known from: [1] the type locality, 20 km SE of Toliara; [2] the area around Morondava, based on a picture made by a German development aid worker and published by MEIER (1986); [3] the Isalo massif (altitude ca. 800 m), based on a personal communication of A. PEYRIERAS and on DALY et al. (1996) The locality Mandena in south-eastern Madagascar, given by GLAW & VENCES (1994), was based on an erroneous information of G. HALLMANN and was corrected by VENCES et al. (1996).

Diagnosis. (1) *Morphology*: A medium-sized, stout *Mantella* SVL 20-26 mm. TTA sometimes reaching only the tympanum, but generally reaching the eye center. Terminal disks of fingers and toes expanded. Mean tympanum/eye ratio nearly 3/5. IMT medium sized (ratio width/length slightly more than 2/3). – (2) *Dorsal color and pattern*: Head and dorsum dirty yellow to lemon yellow with a sharp dorsolateral color border to the black flanks. Limbs grey to bright metallic blue. A thin bluish white frenal stripe present. Iris with light pigment in its upper part. – (3) *Ventral color and pattern*: Black with irregularly shaped blue markings which can fuse to form a blue black marbling. Blue markings present on the breast. Throat largely blue, as a very extended horseshoe marking.

***Mantella manery* n. sp.**

Mantella sp. GLAW & VENCES, 1994, VENCES et al., 1996

Mantella "marojezyi" [conditional name]. STANISZEWSKI, 1996, 1997a, 1997b (e.g. p. 16-18)

Mantella "marojezyi" [conditional name]. STANISZEWSKI, 1997b (p. 61)

Mantella "marojezyi" [conditional name]. LARSEN, 1997.

Name-bearing type – A single specimen of this species was preserved and deposited in the herpetological collection of the Zoological Institute of the Antananarivo University, Madagascar (leg. F. GLAW, N. RABIBISOA & O. RAMILISON, 27.III.1994) and is here designated as holotype. The following description is based on color slides of this specimen

Type locality – Reserve Naturelle Intégrale Marojezy, near Camp 1, ca. 300 m altitude

Other types. – None.

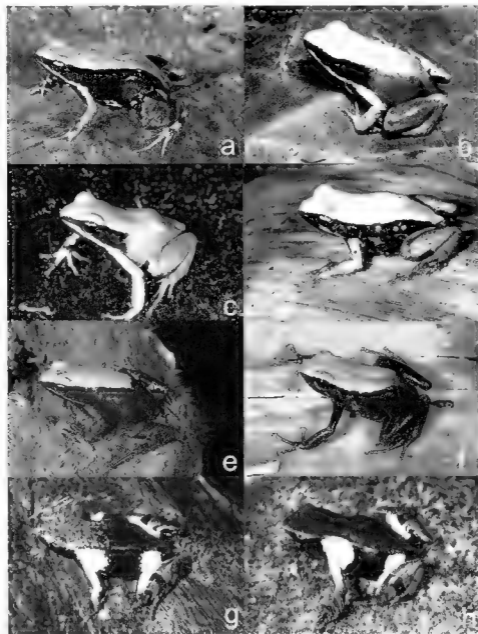


Fig. 1 - Photographs of *Mantella* species (a) *M. betsileo* from Nosy Be (specimen not preserved), 1992, (b) *M.* sp. 1 from Ankarana (specimen not preserved), 1995, (c) *M. viridis*, specimen without locality data (not preserved), 1995, (d) *M. eximicata*, specimen without locality data (not preserved), 1995, (e) *M. maneri* from Marojejy (holotype, deposited in the herpetological collection of the Antananarivo University), 1994, (f) *M. laevigata* from Marojejy (specimen not preserved), 1995 (g-h) *M. nigricans* from Marojejy with and without greenish dorsal color patterns, 1995

Identity. – Color patterns of this species differ from the remaining species of the *M. betsileo* group. Its occurrence in rainforest also differs from most other species of the group (except *M. betsileo*). It was considered a distinct species by GLAW & VENCES (1994). Unfortunately, no specimen of this form was available for detailed examination, as the only preserved specimen is stored in the herpetological collection of the University of Antananarivo. Until present, we thought that the description of this species should wait until new material was collected, and new data on its variation, calls, ecology and osteology became available. However, several hobbyist authors (e.g., STANISZEWSKI, 1996; LARSEN, 1997) have made reference to this form as “*Mantella marojezyi*”, “*Mantella marojezi*” or “*Mantella marojez*”, providing diagnoses which were entirely based on our previously published data. All authors who previously used these names wrote them in quotation marks; these usages thus must be seen as conditional names which are not nomenclaturally available according to article 15 of the *Code*. However, it can be expected that sooner or later the name will be used without quotation marks in any of the increasingly published hobbyist accounts on *Mantella* (see *Discussion* below), accompanied by a diagnosis, and will thus become valid. We therefore prefer to name the form by a formal preliminary description, designating the specimen stored in the Antananarivo collection as holotype. Our preliminary account should be complemented as soon as the holotype (currently not available to us) is examined in detail, and new field observations are made.

Etymology. – Derived from the Malagasy verb *manery* (to force, forced), here used as an invariable substantive standing in apposition to the generic name. We were forced to describe and name this form in a preliminary way to avoid it being named without proper diagnosis in a hobbyist publication.

Distribution. – Only known from the type locality: [1*] Marojezy massif, near Camp 1.

Diagnosis. – The new species is a member of the *M. betsileo* group based on the presence of a horseshoe marking, frenal stripe, dorsolateral color border, and lack of orange/red color ventrally on the hindlimbs. It differs from all species of that group by the rounded light ventral spots (generally at least partly vermiculated in the other species of the group), the brownish posterior dorsum (of same color as anterior dorsum in the other species) and the dark brown dorsal color of fore- and hindlimbs (lighter in the other species). It further differs from *M. betsileo* and *M. sp. 1* by the greenish rather than brown dorsum; from *M. viridis* by the entirely dark brown flanks; and from *M. expectata* by the lack of bluish dorsal color on the dorsal surface of the limbs and the lesser extent of the light ventral spots and markings. (1)

Morphology of the holotype. – Unknown, estimated SVL 25 mm. (2) *Dorsal color and pattern of the holotype*. – Head and anterior part of dorsum yellowish green. Posterior part of dorsum and flanks dark brown. Sharp dorsolateral color border present anteriorly. The yellowish green dorsal color posteriorly ending straight (not semicircularly) and not covering the posterior part of the dorsum. A thin, light, partly interrupted frenal stripe present. Limbs dark brown with a very fine, irregular black dotting. Two dark crossbands on the hindlimb. Iris with light pigment in its upper part. See also color pictures in GLAW & VENCES (1994) and VENCES et al. (1996). (3) *Ventral color and pattern of the holotype*. – Black with a relatively large number of small, regularly rounded blue markings which become smaller anteriorly. Horseshoe marking present.

Mantella sp. 1

Mantella n. sp. 3: CLARK, 1994

Chresonyms

Mantella betsileo BLOMMERS-SCHLÖSSER & BLANC, 1991 (part), GLAW & VENCES, 1992a (part, see localities), 1994 (part; see localities)

Mantella cf. *betsileo* VENCES et al., 1996.

Identity VENCES et al. (1996) first mentioned the presence of this form in Ankarana, based on the observations of J. KÖHLER. R. NUSSBAUM (personal communication) found it in the spiny desert of southern Madagascar and considered it as a species distinct from *M. betsileo*.

Comment No scientific name is currently disponible for this form. Formal description of this species will be the subject of a forthcoming paper

Material examined - ZFMK 61238-41 and ZFMK 62197-9 (Ankarana; leg. J. STEINBRECHER 1995, 61241- CS) Several MNHN specimens can also be referred to this species MNHN 1973 484-96 (Androatsalo), MNHN 1973 497 (Tongahybe [Baly-Ouest]), MNHN 1973 498 (Androatsalo), MNHN 1976 214-8 (Morondava; SVL 26.4 mm [214], 23.3 mm [215], 26.1 mm [216], 21.7 mm [217], 22 mm [218]) The specimens MNHN 1973 217-8 may also belong to *M. betsileo* which is known from Kirindy near Morondava (KUCHLING, 1993, GLAW & VENCES, 1994). Due to the large size of the specimens MNHN 1976.214 and MNHN 1976 216, we here refer the whole series to *M. sp. 1*. We also refer to the species in a preliminary way a BMNH series. BMNH 74 10 29 1 4 (Mohambo, purch. M. BOUCARD, NIL, four females, SVL 26.5 mm, 25.9 mm, 25.4 mm, 21.0 mm, no light spots in thorax region)

Several other MNHN specimens with unknown localities may be referred to *M. sp. 1* based on their large size: MNHN 1976 183-6 (SVL 23.2 mm [183], 24.6 mm [184], 26.6 mm [185], 26.9 mm [186]); MNHN 1976 188 (SVL 23.6 mm), MNHN 1976 191 (SVL 24.2 mm), MNHN 1976 193 (SVL 27.3 mm), MNHN 1976 194 (SVL 25.1 mm), MNHN 1976 197 (SVL 24.5 mm), MNHN 1976 198 (SVL 26.4 mm), MNHN 1976 199 (SVL 27.1 mm)

Distribution [1] Ankarana; [2] Tongahybe; [3] Morondava, [4] Androatsalo (Androatsabo according to BLOMMERS-SCHLÖSSER & BLANC, 1991); [5] Mohambo (locality not traced and not included in map) According to NUSSBAUM (personal communication, see also CLARK 1994), large populations of this species occur in the spiny desert of south-western Madagascar.

Diagnosis - (1) **Morphology**. A large, rather stout *Mantella* SVL 22-30 mm, males 25 mm, females 29-30 mm. TTA reaching the posterior eye margin in small specimens (males), between forelimb insertion and tympanum in large females. Terminal disks of fingers and toes slightly expanded. Mean tympanum/eye ratio nearly 3/5. IMT medium sized (ratio width/length about 2/3). (2) **Dorsal color and pattern** Dorsal head surface and dorsum yellowish to light brown, mostly without diamond marking. Sharp dorsolateral color border anteriorly present. Flanks black, with fiery red color extending posteriorly. White frenal stripe present. Limbs brown to red-brown, with at least one dark brown crossband on femur, tibia and tarsus. Iris with light pigment in its upper part. - (3) **Ventral color and pattern**: Black with blue markings, of different size and extension but often showing vermiculated patterns and fusing with each other. Breast region generally without or with only very small light markings. Distinct horseshoe marking present, sometimes including a central stripe

Mantella viridis Pintak & Böhme, 1988

Mantella viridis Pintak & Böhme, 1988 *Name-bearing type*: holotype by original designation (PINTAK & BÖHME, 1988: 120), ZFMK 47900, female, SVL 30.3 mm – *Type locality*: “südlich Antseranana (= Diego Suarez), Nord-Madagaskar”, according to original description. *Other types*: 11 (lost) paratypes (see comment below) – *Etymology*: derived from Latin *viridis* (green).

Mantella viridis: PINTAK, 1990, OLIVETTI, 1990 (fig.); BLOMMERS-SCHLOSSER & BLANC, 1991 (p. 274), ZIMMERMANN, 1992, GARRAFFO et al., 1993, ANDREONE, 1992 (plate III fig. 5-6), GLAW & VENCES, 1992a, 1994, HERRMANN, 1993 (fig. 1), LE BERRE, 1993 (fig. p. 20), ZIMMERMANN & ZIMMERMANN, 1994, BARTLETT, 1995 (fig. p. 17), HENKEL & SCHMIDT, 1995 (fig. p. 57), CARISSIMI-PRIORI, 1995 (fig. p. 43), VENCES et al., 1996, 1998, DALY et al., 1996, 1997a, STANISZEWSKI, 1997b (fig. p. 6), LARSEN, 1997; PINTAK et al., 1998; VENCES & KNIEL, 1998.

Mantella spec.: VAN TOMME, 1988 (fig. 2)

Other chresonyms:

Mantella betsileo: BUSSE, 1981 (part.); BLOMMERS-SCHLOSSER & BLANC, 1991 (part.), GLAW & VENCES, 1992a (part.; see localities), 1994 (part.; see localities)

Mantella expectata: STANISZEWSKI, 1997a (fig. p. 12).

Comment – In the original description (PINTAK & BÖHME, 1988), 11 living, uncatalogued specimens (four males and seven females, with same locality data as holotype) were designated as paratypes. No specimens of this captive stock were eventually preserved and catalogued; all paratypes must therefore be considered as lost.

Material examined: ZFMK 47900 (according to catalogue Mige d’Ambre, S of Diego [Antseranana], leg. D. BRÉZ 1987, holotype), ZFMK 48038-53 (Antseranana [Diego Suarez]; leg. H. MEJER III 1988, 48048 CS), ZFMK 62708-9 (locality unknown, CS); ZFMK 62710-2 (locality unknown, TE), MRSN A416 (locality unknown; through the pet trade).

Three specimens (MNHN 1976 211-3, Montagne des Français) are also referred to *M. viridis* based on their locality, size and relative hindlimb length. They clearly cannot be attributed to *M. betsileo* as in the MNHN catalogue, but due to the faded colors we cannot completely exclude their belonging to *M. sp. 1*. MNHN 1992.4820 (locality unknown) is here also referred to *M. viridis* based on size and relative hindlimb length, although color patterns are not recognizable any more.

Distribution. Only known from the northern tip of Madagascar. The published type locality is south of Antseranana. The only reliable localities known are: [1] 13 km south of Antseranana (DALY et al., 1996); [2*] Montagne des Français (GLAW & VENCES, 1994; ca. 100-300 m altitude), south of Antseranana. ZFMK specimens with the locality “Antseranana” were most probably collected in the Montagne des Français. ANDREONE (1992) showed pictures of *Mantella viridis* from “area of Montagne d’Ambre National Park” (plate III fig. 5-6), but previously stated (p. 423) that he had not observed the species in nature and that locality information was based on PINTAK & BÖHME (1988). Most probably the species is not present in the Montagne d’Ambre National Park since recent surveys failed to find it (RAEWORTHY & NUSSBAUM, 1994; GLAW & VENCES, 1994).

Diagnosis. (1) *Morphology*: A large, rather stout *Mantella*. SVL, males 22-25 mm, females 27-30 mm, TTA reaching the eye center in many specimens (mostly males), but only the forelimb insertion in large females. Terminal disks of fingers and toes expanded. Mean tympanum/eye ratio about 2/3. IMT medium sized (ratio width/length slightly less than 2/3).

(2) *Dorsal color and pattern*: Head, dorsum and largest (posterior) part of the flanks light green to yellowish. Anterior part of the flanks black, this color reaching in many specimens to a point around the forelimb insertion. A sharp dorsolateral color border present in this area.

Distinct, white to light green frenal stripe present. Color of limbs generally similar to dorsum, without a dark crossband, but hindlimbs with a metallic blue shade in some specimens. Iris with light pigment in its upper part. (3) – *Ventral color and pattern*: Black with bluish white markings decreasing in size from posteriorly to anteriorly, generally absent on the breast. Markings of irregular shape, often vermiculate and fusing with each other. Distinct horseshoe marking present on the throat.

Mantella laevigata group

Mantella laevigata Methuen & Hewitt, 1913

Mantella laevigata Methuen & Hewitt, 1913 – *Name-bearing type*: holotype by original designation (METHUEN & HEWITT, 1913: 58), TM 10074 (ex 1214), sex unknown, SVL 22.5 mm. *Type locality*: “Folohy”, according to original description and TM catalogue. *Other types*: six paratypes according to original description (ex 1212, 1215-9), TM 10085-8, TM 10090 and MCZ 10815 (see comment below). *Etymology*: derived from Latin *laevigare* (to make smooth).

Mantella laevigata GUIBÉ, 1964 (syn. *cowani*), 1978 (syn. *cowani*); BUSSÉ, 1981; MEIER, 1986; PINTAK, 1990; BLOMMERS-SCHLÖSSER & BLANC, 1991; ANDREONE, 1992 (plate IV fig. i-2); GLAW & VENECES, 1992a, b, 1994; GARRAFFO et al., 1993; HIRRMANN, 1993 (fig. 1); LE BERRE, 1993 (fig. p. 20); HENKEL & SCHMIDT, 1995 (fig. p. 54); BARTLETT, 1995 (fig. p. 24); DALY et al., 1996; STANISZEWSKI, 1997a (fig.), 1997b (fig.), 1998a (fig.); LARSEN, 1997; GLAW et al., 1998a; PINTAK et al., 1998; VENECES et al., 1998; VENECES & KNIEL, 1998.

Other chresonyms:

Mantella cowani: GUIBÉ, 1964 (part.), 1978 (part.).

Mantella madagascariensis: BLOMMERS-SCHLÖSSER & BLANC, 1991 (part. included in syntype series of subspecies *M. m. nigricans*, locality Marojezy, same applies to BUSSÉ, 1981, and GLAW & VENECES, 1992a, 1994).

Pictured in MEIER (1980: fig. p. 353 below) as “Bisher nicht eindeutig einzuordnende *Mantella*-Art”.

Comments: (1) The holotype is in good state of preservation. The pattern is largely faded but still recognizable on head and anterior dorsum. A few of the light ventral spots are still recognizable; they are small and rounded. The paratypes TM 10085-6 are in a rather bad state of preservation; the pattern contrast is largely faded, and the ventral pattern is not recognizable. TM 10088 and 10090 are also in bad state of preservation with faded pattern, but they can clearly be assigned to *M. laevigata* by their broad finger disks. TM 10087 is in good state of preservation, pattern contrast is weak, but both dorsal and ventral (small rounded spots) pattern is still recognizable. (2) Seemingly, the type locality “Folohy forest” does not exist any more; its location was traced by BLOMMERS-SCHLÖSSER & BLANC (1991) immediately north of Toamasina (Tamatave), and we follow this placement in our distribution maps. (3) Barbour & Loveridge (1929) mentioned the existence of one “syntype” in the TM and one in the MCZ (MCZ 10815). However, the original description (a) clearly stated that it was based on “seven examples”, listed as “1212, 1214-1219” and (b) separately mentioned specimen 1214 once more, as “type”. Although not explicitly stated, this infers the existence of one holotype (ex 1214, today TM 10074); we consider all additional specimens listed in the original description as paratypes. MCZ 10815 is almost certainly the specimen formerly numbered TM 10089, which was exchanged with MCZ, according to the TM catalogue, on

8 VII 1925. (4) Whereas the locality of the holotype and of the paratypes TM 10087-8 and MCZ 10815 is Fohohy, that of the paratypes TM 10085-6 and 10090 is only "E Madagascar", according to the TM catalogue.

Material examined. TM 10074 (Fohohy, Eastern Madagascar; coll. by HERSCHELL-CHAUVIN, 1911, holotype), TM 10085-6 and 10090 (Eastern Madagascar resp. East region, Malagasy Republic; coll. HERSCHELL-CHAUVIN, 1912, paratypes), TM 10087-8 (Fohohy, E-Madagascar; coll. HERSCHELL-CHAUVIN, 1912, paratypes); BMNH 1952.11 53-54 (Mangabe island, Antongil bay, coll. C. S. WEBB, NIL), MNHN 1973.534-40 (Marojezy, 300 m, paralectotypes of *M. nigricans*), MNHN 1973.542-7 (Marojezy, 300 m, paralectotypes of *M. nigricans*), MNHN 1973.549 (locality unknown, paralectotype of *M. nigricans*), MNHN 1973.557.8 (Marojezy, 600 m, paralectotypes of *M. nigricans*); two juvenile specimens of the MNHN collection most probably also belong to *M. laevigata* MNHN 1973.517 (Marojezy 300 m, SVL 12.3 mm, paralectotype of *M. nigricans*), MNHN 1973.548 (Marojezy 300 m, SVL 12.1 mm, paralectotype of *M. nigricans*); ZFMK 19298 (Maroantsetra, leg. H. MEIER 1976), ZFMK 48660 (Nosy Mangabe, leg. R. ZOBEL VI 1988); ZFMK 52747-51 (Nosy Mangabé, leg. F. GLAW & M. VENCES III 1991; 52749 CS), ZFMK 59911 (Marojezy Camp 1; leg. F. GLAW & O. RAMILISON II 1995), ZFMK 59912 (Marojezy Camp 2, leg. F. GLAW & O. RAMILISON II 1995; juvenile), ZFMK 59913-4 (Marojezy Camp 3, leg. F. GLAW & O. RAMILISON II 1995), ZFMK 62786-8 (locality unknown, TE), MRSN A0065.1-3 (Nosy Mangabe, leg. F. ANDREONE 24 IV 1990), MRSN A1826 (Tsararano Chain Camp 1, leg. F. ANDREONE 4 XII 1996), MRSN A1827, MRSN A1828 1-2 (Tsararano Chain, Camp 2 leg. F. ANDREONE 13-14.XII.1996).

Distribution. - [1] Type locality Fohohy. Recent localities from the East and North-East are. [2*] the small island Nosy Mangabe (100-300 m altitude); [3] the Tsararano chain (700 m altitude); [4*] the Marojezy massif (300-700 m altitude). Two additional localities from the northern part of the Eastern Region are found in DALY et al. (1996): [5] Ambodimanga and Varary, both in the Mananara reserve (ca. 100 m altitude). The locality Maroantsetra (based on ZFMK 19298, see BUSSE, 1981) does almost certainly not refer to the town Maroantsetra itself but to a nearby locality (most probably Nosy Mangabe) and is therefore not accepted here.

Diagnosis. - (1) *Morphology:* A medium sized to large *Mantella* with a generally very slender appearance. Terminal disks of fingers and toes largely expanded. SVL 22-29 mm. TTA reaching generally the eye center and slightly beyond the eye in some specimens. Tympanum/eye ratio between 1/2 and 3/5. IMT medium sized (ratio width/length about 3/5).

(2) *Dorsal color and pattern:* Head and anterior part of dorsum covered by a sharply delimited yellow mark, posteriorly either ending semicircularly or prolonged as a pointed triangle to the cloacal region, with a sharp dorsolateral color border to the black flanks and sides of head. Variation in shape of dorsal yellow mark not corresponding to sexual dimorphism. Limbs deep black (exceptionally copper brownish). Hands and finger tips often with blue spots. No frenal stripe, but single yellowish spots sometimes present under the eyes. No flashmarks. Iris completely black without light pigment. - (3) *Ventral color and pattern:* Venter and limbs black with small, rounded, bluish or bluish-grey spots. Throat generally completely black without pattern (few light spots sometimes present). No red, orange or yellow pattern on hindlegs.

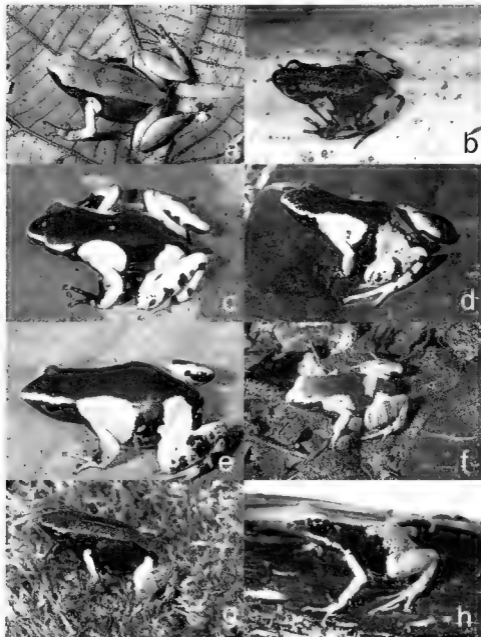


Fig 2. Photographs of *Mantella* species. (a) *M. baraldmeieri* from Nahampoana 1991, (b) *M. conanti*, specimen without locality data (not preserved) 1994 (c) *M. baroni*, specimen without locality data (not preserved, but belonging to the same series as ZFMK 62718-75), 1997, (d) *M. all. baroni* from Andringitra (ZMA 6754), photograph taken from BLOMMERS-ST. HOUSSER & BLANC (1993), (e) *M. malagascariensis*, specimen without locality data (not preserved, but belonging to the same series as ZFMK 62732-41), 1997, (f) *M. pulchra*, specimen without locality data (not preserved), 1994, (g) *M. bernhardi* from near Tolongoina (holotype ZFMK 57164), 1994, (h) *M. crocea*, specimen without locality data (ZFMK 52746), 1991

Mantella cowani group**Mantella baroni** Boulenger, 1888

Mantella Baroni Boulenger, 1888 *Name-bearing type* holotype by monotypy, BMNH 1947 2 7 19 (ex 84 12 22 50), male (according to the original description), SVL 27.2 mm *Type locality* not specified in the original description, "Madagascar" without further specifications according to the BMNH catalogue - *Etymology* named after the collector of the type, Reverend P. BARON

Mantella Baroni: MOCQUARD, 1909.

Mantella baroni WERNER, 1901, MATHUEN & HEWITT 1913, PARKER, 1925, GUIBÉ 1964, 1978 (syn. *cowani*), BUSSI, 1981 (syn. *madagascariensis*), BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn. *madagascariensis*); GLAW & VENCES, 1994 (syn. *madagascariensis*, p. 412); DALY et al., 1996, 1997b, PINTAK et al., 1998, VENCES et al., 1998, VENCES & KNIEL, 1998, STANISZEWSKI, 1998a (fig. 1)

Phrynomantis maculatus Thoinot, 1889 - *Name bearing type* lectotype (designated by GLAW & VENCES, 1994) MNHN 1991 2845 (ex 6807a), sex unknown, SVL 27.0 mm. *Type locality* "Île de La Reunion" according to original description (probably erroneous, see comment below) *Other types* paralectotypes MNHN 1991 2846 (ex 6807b), MNHN 1991 2847 (ex 6807c) and MNHN 6807 *Etymology*: derived from Latin *maculatus* (spotted)

Phrynomantis maculatus GUIBÉ, 1964, 1978 (syn. *cowani*), BUSSI, 1981 (syn. *madagascariensis*), BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn. *madagascariensis*), GLAW & VENCES, 1994 (syn. *madagascariensis*; p. 413)

Other chrysonyms:

Mantella cowani, GUIBÉ, 1964, 1978 (part.), MATZ, 1975 (fig. 1), MEIER, 1975 (fig. 1-2), MEIER, 1980 (fig. p. 352), OBERLE, 1981 (pl. 29), LE BERRE, 1993 (part., outer fig. p. 21)

Mantella madagascariensis BEUTELSCHESS & BEUTELSCHESS, 1987, PINTAK, 1990 (part.), OLIVETTI, 1990 (fig. 1), BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), ANDREONE, 1992, GLAW & VENCES, 1992b (fig. p. 28), ZIMMERMANN & ZIMMERMANN, 1992 (fig. 5 21), GARRAJO et al., 1993, CLARK, 1994 (fig. p. 10 below), VENCES et al., 1994 (fig. p. 390) GLAW & VENCES, 1994 (part.), BARTLETT, 1995 (fig. p. 18 below right); HENKEL & SCHMIDT, 1995 (fig. p. 55), CARISSIMI-PRIORI, 1995 (fig. p. 42); STANISZEWSKI, 1996 (plate p. 16-17); 1997a (fig. p. 12), 1997b (fig.), ZIMMERMANN, 1996b (fig. 14)

Mantella madagascariensis sensu stricto: GLAW & VENCES, 1992a (part.; see localities)

Mantella madagascariensis madagascariensis BUSSI, 1981 (part.), MEIER, 1980 (fig. 6), VAN TOMME, 1988 (fig. 5-6); ANDREONE & GAVETTI, 1993 (p. 105).

Identity - BUSSI (1981) defined *M. madagascariensis* as a very variable species containing several junior synonyms, including *M. baroni*. One main problem with this definition was the bad state of preservation of the *M. madagascariensis* types (see below) which made reliable attribution of this name to any specific morph impossible. Recent studies have shown that many of the forms previously summarized under the name *M. madagascariensis* do in fact belong to separate well-defined, valid species (GLAW & VENCES, 1994). Two morphs (here named A and B) remained without an unequivocal definition. morph A, figured on plate 61 in GLAW & VENCES (1994), was considered as *M. madagascariensis*, whereas the "variable" morph B, figured on plates 58-59 in GLAW & VENCES (1994), was considered as *M. "loppet"* in a preliminary way. GLAW & VENCES (1994) mentioned that morph A corresponds to the type of *M. baroni* which they listed as synonym of *M. madagascariensis*. DALY et al. (1996), referring to this definition, argued that *M. baroni* should be revalidated as a valid name (for morph A), whereas the name *madagascariensis* should be seen as "nomen dubium" due to the bad state of the type specimens.

We here follow these conclusions as far as the definition of morph A as *Mantella baroni* is concerned. *M. madagascariensis*, however, is not "unidentifiable" (DALY et al., 1996); a new, detailed examination of the lectotype of that taxon showed that it corresponds to morph B (see corresponding section).

Comments - (1) The holotype of *M. baroni* is in rather bad state of preservation, but the relevant color patterns can still be recognized. (2) According to BLOMMERS-SCHLÖSSER & BLANC (1991), the number BMNH 1947.2.7 19 defines "syntypes" of *M. baroni*; however, BOULENGER (1888) in his original description mentioned explicitly "a single male specimen". We found no indications on the existence of types other than a single holotype in the BMNH collection and catalogue. The specimens ZFMK 28770-28772 cannot be seen as *M. baroni* "paratypes" as was suspected by BUSSE (1981); their collecting data agree with those of the series BMNH 95.7.4.34-6 and 96.12.2.28-31, but not with those of the holotype. - (3) The type locality of *Phrynomantis maculatus*, according to the original description, is "Île de La Réunion". BUSSE (1981) first gave the locality "Nosy Cumba-Nosy Be" without providing additional information nor his source of information. This locality was subsequently also given by BLOMMERS-SCHLÖSSER & BLANC (1991) but was questioned by GLAW & VENCES (1994). According to A. ÖHLER (in litt., 1997), a second MNHN catalogue informs that the specimens were supplied by the "Com. scientifique de Bourbon" (Bourbon is an old name for the island of La Réunion). This explains the wrong locality information "Réunion", which was later corrected to "Nossi-Be et Nossi-Cumba" in one MNHN catalogue, and to "Madagascar" in a second catalogue. We consider also the Nosy Be - Nosy Komba locality information as wrong (see below).

Material examined - BMNH 1947 2 7 19 (holotype, Madagascar, leg. R. BARON), BMNH 95 7 4 34-6, BMNH 96 12 2 28-31 (Ambohitombo forest, coll. FORSYTH MAJOR [1 specimen exch. Vienna 1912], NIL), BMNH 1925 7 13 1-6 (Madagascar, coll. FORSYTH MAJOR, NIL), BMNH 1925 7 2 57 (Antsihanaka, purch. ROSENBERG), BMNH 1930.2 7.1 (Analamazoatra forest, environs of Périnet, purch. ROSENBERG), BMNH 1953 1 5 42-5 (Madagascar, pres. G. W. ALLAN), MNHN 6807, MNHN 1991 2846-7 (ex MNHN 6807, "Nosy Komba", paralectotypes of *Phrynomantis maculatus*), MNHN 1991.2845 (ex MNHN 6807A; lectotype of *Phrynomantis maculatus*, "Nosy Komba"); MNHN 1883.584 (locality unknown, ded. HUMBLOT), MNHN 1902 335 (Ikongo; M. Bensch), MNHN 1907.161-2, MNHN 1991 1813 (locality unknown, obtained from the "section de Madagascar à l'Exposition coloniale de Marseille", ex MNHN 1907 162, 162A); MNHN 1931 14 (locality unknown), MNHN 1991 1807 9 (locality unknown, ex MNHN 1931 14 A-C), MNHN 1931 15 (Moramanga), MNHN 1991 1810-2 (Moramanga, ex MNHN 1931 15 A-C), MNHN 1931.16-7 (SF Fianarantsoa, DUCARY 1926-1930), MNHN 1933 247 (Ruisseau d'Iorantatsy, Distr. Fianarantsoa, alt. 1000 m), MNHN 1936 40-2 (Forêt de Tsianovoaha), MNHN 1936 43-6 (probably "forêt de Tsianovoaha", HEIM), MNHN 1953 135 (Anosibe [Moramanga]), MNHN 1972 775-6 (Moramanga), MNHN 1976 233-4 (locality unknown); MNHN 1988 7599 (locality unknown, don. O. BIERA III 1988), MNHN 1993 1441-2, MNHN 1993 1444, MNHN 1993.1446-7 (locality unknown), ZFMK 14208 (Niagarakely, leg. H. MEIER 1972), ZFMK 28870-2 (Ambohitombo forest; leg. FORSYTH MAJOR 1903, originally Museum Göttingen), ZFMK 46035-8 (locality unknown, through pet trade, 46035 CS), ZFMK 47008-9 (Moramanga, leg. R. SHIPP IV 1987), ZFMK 48054-60 (120 km S Moramanga Marolamba, leg. H. MEIER III 1988, 48055 CS), ZFMK 50161 3 (Moramanga, leg. H. MEIER II 1989), ZFMK 50551 (Moramanga, leg. F. W. HINKEL, W. SCHMIDT & V. MILLER 1989), ZFMK 56165-9 (through pet trade, ded. F. GLAW XI 1993), ZFMK 62242 (Mantady, leg. F. GLAW II 1996), ZFMK 62718-21 (locality unknown, CS), ZFMK 62722 5 (locality unknown, TE), ZFMK 62287-8 (juveniles) and 641 39-40 (all Vohparara, leg. F. GLAW, D. RAKOTOMALALA & F. RANAIVOAJONA III 1996, TF), MRSN A0061 1-4 (Andasibe, Amalonahe, leg. F. ANDRIONO 2 XII 1991), MRSN A0066 1-5 (Vatoharanana-Ranomafana, c/o Ifanadiana, leg. F. ANDRIONO 8 II 1993, NIL), MRSN A0067 1 5 (Vohparara, leg. F. ANDRIONO 9 II 1993), TM 9890, 9896, 9900 (Analamazoatra, leg. METHUEN).

The following somewhat deviating specimens are also attributed to *M. baroni* in a preliminary way (see discussion below): TM 9888 9, 9892, 9895, 9898-9 (Folohy, coll. MEHTEN), TM 9894 (Folohy, coll. HERYCHILLI CHAU VIN), BMNH 1986 2 (Camp 4, Zahamena, 17°40' S, 48°50' W, leg. C. J. RAXWORTHY 8 IX 1985).

Distribution The species of the *M. cowani* and *M. madagascariensis* groups (as defined in the present study) were insufficiently distinguished in previous works. The corresponding distribution maps (mainly in BLOMMERS-SCHLOSSER & BLANC, 1991, as *M. madagascariensis* and *M. cowani*) did not contain references to literature records or voucher specimens. GLAW & VENCES (1994) assigned some localities to the species *haraldmeieri*, *cowani*, *pulchra* and "loppei", but most localities remained without reliable attribution to any species.

The distribution map of BLOMMERS-SCHLÖSSER & BLANC (1991) was mainly based on MNHN voucher specimens. All of these were examined by us. This allows us for the first time to outline the distribution of the different species with a certain reliability. *M. baroni* occurs in the central Eastern Region, mainly at mid-altitude localities: [1] Antsihanaka; [2*] Ankeniheny (ca 1000 m altitude), [3*] An'Ala (ANDREONE, 1993, DALY et al., 1996; personal observation at ca 840 m altitude); [4*] Analamazoatra; [5] Anosibe (Anosibeana); [6] Niagarakely; [7] Marolamba (120 km S Moramanga; probably identical with Marolambo, which is situated about 100 km S Moramanga, see BLOMMERS-SCHLÖSSER & BLANC, 1993); [8] Ambohimombo; [9] Ikongo; [10] Ruisseau d'Iorantjatsy; [11] Forêt de Tsianovoha, [12*] Ranomafana National Park (ANDREONE, 1992; GARRAFFO et al., 1993; personal observation near Vohiparara, ca. 1000 m altitude), [13*] Mantady. Additional localities were published by DALY et al. (1996) [14] Sahavondrona (near Ranomafana; ca 1000 m altitude), [15] 30-35 km south of Moramanga.

Two additional localities, [17] Folohy and [18] Zahamena (TM and BMNH vouchers, see above) are attributed to *M. baroni* only in a preliminary way. These specimens, which unfortunately have largely faded color patterns, show a deviating coloration which resembles *M. nigricans* in many respects. In the Folohy sample, the ventral side including the femur is dark with small (not large as usually in *M. baroni*) rounded light spots (no horseshoe marking). The tibia and the foot are light (except TM 9888 which has a dark tibia). The flank blotches are large and rounded, as typical for *M. baroni*. The rostral stripe appears indistinct without sharp borders, and the head surface may have been lighter than the back in life. The single known Zahamena specimen, according to the attached field label, had the following life coloration "Back and legs vivid bright green, flanks black, lower back and legs brown, belly black with pale blue spots, iris black". In preservative, the pattern is largely faded. Femur and tibia are dark, but the foot is light ventrally and dorsally. The existing information on these specimen does not allow for further statements, in the distribution map, we list the two localities as intermediate between *M. baroni* and *M. nigricans*. The color and pattern information given below for *M. baroni* applies to all populations except for Folohy and Zahamena.

The remaining localities listed by BLOMMERS-SCHLOSSER & BLANC (1991) for *M. madagascariensis* can be assigned as follows: Marojezy refers to *M. nigricans*. Antsihanaka is the type locality of *M. pulchra*. Marolambo is the type locality of *M. loppei* (junior synonym of *M. madagascariensis* according to the present study), and seems also to be a locality of *M. baroni* (see above, if Marolambo and Marolamba are identical). Ambalavato is the type locality of *M. madagascariensis*, Itremo, Ambatodradama and Betafo refer to *M. cowani*. Chaînes Anosyennes, Ambana, Bekazaha and Soavala refer to *M. haraldmeieri*, Ivohibe and Marovitsika refer to *M. aff. baroni* which is here considered separately (see below).

We propose to delete the localities Nosy Be and Nosy Komba (which are based on a dubious locality information referring to the types of *Phrynomantis maculatus*, see above). As discussed by GLAW & VENCES (1994), these localities are in the Sambirano region where recent extensive surveys have only yielded records of species of the *M. betsileo* group. We also propose to ignore the locality Ambohidratrimo, located 20 km NW of the Malagasy capital Antananarivo (VILITTE, 1991) near the Ivato airport. No vouchers for this locality were found in the MNHN. The presence of habitat structures suited for species of the *M. baroni* group or *M. madagascariensis* group is not probable at this locality for the last 100 years.

Diagnosis. - (1) *Morphology*: A large, slender *Mantella*. SVL 22-30 mm. TTA mostly reaching the eye center but at least the tympanum. Terminal disks of fingers and toes expanded. Tympanum/eye ratio generally 3/5. IMT small (ratio width/length about 4/5). - (2) *Dorsal color and pattern*: Head, dorsum and flanks deep black, without dorsolateral color border. Frenal stripe absent. Yellowish rostral stripe present, generally not in contact with flank blotch. Forelimb (except the mostly black fingers) and femur yellow to greenish. This color continuing onto the flanks, forming relatively large, rounded flank blotches. These sometimes dorsally expanding onto the back, not being delimited by the dorsolateral border. Size of blotches variable, but in none of the examined specimens blotches of opposite flanks contacting each other on the back. Tibia, tarsus and foot orange with irregular black crossbands and markings. No flashmarks. Iris completely black without light pigment. - (3) *Ventral color and pattern*: Venter, throat and limbs black with few relatively large, rounded light markings which are generally not blueish but yellow to greenish. No horseshoe marking, throat with only a single rounded marking, sometimes completely black. Tibia, tarsus and foot orange as dorsally, but mostly without black patterns. The orange color sometimes reaching the distal part of the femur but not further proximally. Exceptionally, single specimens with a nearly complete horseshoe marking (observed in one specimen of the series MRSN A0066).

***Mantella* aff. *baroni* (from Andringitra)**

Chresonyms:

Mantella covarr GUIBÉ, 1964 (part.: fig. 4-6), 1978 (part.)

*Mantella madagascariensis** BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), 1993 (pl. 19 fig. 104); GLAW & VENCES, 1994 (part.)

Mantella madagascariensis sensu stricto GLAW & VENCES, 1992a (part., see localities and fig. 180)

*Mantella madagascariensis madagascariensis** BUSSE, 1981 (part.: fig. 5)

Identity. Within and between the known populations of *Mantella baroni*, the dorsal and ventral coloration of adults as described above is rather uniform (see also ANDRIONGI, 1992; GLAW & VENCES, 1994). On the contrary, specimens from Andringitra (south of all other known localities of *M. baroni*) differed by an enormously variable dorsal pattern (see below). We here consider the Andringitra population as a separate form *Mantella* aff. *baroni* which clearly is very closely related to *M. baroni*. Final clarification of its status is not possible at present.

Comment. - No scientific name is currently dispoible for this form

Material examined – The following specimens can clearly be assigned to this form due to their largely extended dorsal green-yellow pattern MNHN 1953 136 (Col d'Ivohibe, Andringitra), MNHN 1991 1800-4 (Col d'Ivohibe, Andringitra; ex MNHN 1953 136 A-E); MNHN 1972 767, MNHN 1972 769-72, MNHN 1972 774, MNHN 1972 777-8 (Col d'Ivohibe, forêt Marovitsika)

Several other specimens differ from typical *M. baroni* only by a gradually larger extension of the yellow pattern. These are MNHN 1991 1805-6 (Col d'Ivohibe, Andringitra, ex MNHN 1953 136 G-H); MNHN 1972 763-6 (Col Ivohibe, forêt Marovitsika), MNHN 1972 768, MNHN 1972 773 (Col Ivohibe, forêt Marovitsika) MNHN 1991 1805 is most similar to typical *M. baroni* by dorsal pattern. MNHN 1972 763-5 are very large and stout specimens, probably females.

Distribution – Only known from the Col d'Ivohibe [1] in the Andringitra massif.

Diagnosis (1) *Morphology*: A large, slender *Mantella*. SVL 27-31 mm, females 30 mm. TTA reaching eye center in some specimens, but only to forelimb insertion or slightly beyond in large females. Terminal disks of fingers and toes expanded. Tympanum/eye ratio generally 1/2 to 3/5. IMT small. (2) *Dorsal color and pattern*: In some specimens similar to typical *M. baroni*, but with a larger extension of the yellow flank blotches which reach widely onto the dorsum (coloration observed in all specimens identified as females). Other specimens, by general body proportions possibly mainly males, showing a broad dorsal contact of the flank blotches, or a further increase of these, resulting in a nearly uniformly yellow pattern dorsally (see GUIBF, 1964 fig. 4-6, BUSSE, 1981: fig 5), with the yellow color also extending onto the tibia, which is otherwise orange with black. No flashmarks. Iris seemingly with some light pigment in its upper part according to the color plate in BLOMMERS-SCHLÖSSER & BLANC (1993, here reproduced in black-and-white on fig. 2) which shows a specimen relatively similar to typical *M. baroni*, with a (very indistinct) dorsolateral color border. Rostral stripe present and generally in contact with the flank blotches. In specimens with large extension of yellow color, the rostral stripe is the sharp border between yellow dorsal and black lateral color of the head. (3) *Ventral color and pattern*: Similar to *M. baroni*, but with a higher number and smaller size of light markings (intermediate between *M. baroni* and *M. haraldmeieri*). Information on the color of the light markings in life not available.

Mantella cowani Boulenger, 1882

Mantella cowani Boulenger, 1882. *Name-bearing type* lectotype by present designation, BMNH 1947 2 7 4 (ex BMNH 82 3 16 38), female according to BOULANGER (1882), SVL 28 2 mm. *Type locality*: "East Betsileo", according to the original description and the BMNH catalogue. *Other types* paralectotype following present lectotype designation, BMNH 1947 2 7 5 (ex BMNH 82 3 16 39), female according to BOULANGER (1882). *Etymology* named after the collector of the type series, Reverend W. DEANS COWAN.

Mantella cowani DALY et al., 1996; STANISZEWSKI, 1998a (fig.)

Mantella cowani MOCQUARD, 1909

Mantella cowani WERNER, 1901; MITHUN & HEWITT, 1913; PARKER, 1925; GUIBF, 1964, 1978 (part.)
BUSSE, 1981 (syn. *madagascariensis*), BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.); BOHME et al.
1991; VENCES et al., 1994; GLAW & VENCES, 1994; BARTLETT, 1995 (fig. p. 24); CARISMI PRIORI
1995 (fig. p. 43); STANISZEWSKI, 1997a (fig.), 1997b (fig.); LARSEN, 1997; VENCES & KNIE, 1998

Mantella cowani s. str.: ANDREONE, 1992 (p. 438).

Other chresonyms

Mantella madagascariensis: BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.)

Mantella madagascariensis madagascariensis: BUSSE, 1981 (part.)

Mantella madagascariensis nigricans: BUSSE, 1981 (part., MNHN 9594 on p. 33)

Mantella madagascariensis (color morph. *Mantella "cowani"*): GLAW & VENCES, 1992a

Identity. – See BÖHME et al. (1993) and VENCES et al. (1994) for the confusing taxonomic history of the taxon. The species is well distinguished by its typical pattern.

Comments. – (1) Lectotype and paralectotype are in excellent state of preservation. The typical pattern is still recognizable, although the red color has largely faded – (2) Although the specific name was written *cowanii* in the original description, we here continue using the spelling *cowani* which was used by most subsequent authors, since the *Code* allows both spellings to be used.

Material examined. BMNH 1947 2 7 4-5 (lectotype and paralectotype, E-Betsileo, leg. W. D. COWAN); MNHN 1906 171, MNHN 1991 2844 (Betafo), MNHN 1973 528-9 (Ambatomenaloaha, massif Itremo); MNHN 9594 (Ambatodradama, 2000 m, ARNOULT 11 XII, 1962), ZFMK 59822 (locality unknown, ded. F. GLAW IV, 1995), ZFMK 62726-7, ZFMK 62729-31 (locality unknown, TE), ZMB 10404, ZMB 50106-7 (East-Betsileo; leg. HILDEBRANDT).

Also the following specimens with unknown locality are considered as *M. cowani* based on unpublished electrophoretic and morphometric data: ZFMK 62728 (TE, color in life yellow/black instead of red/black); ZFMK 62719, ZFMK 62721 (TE, color in life yellow/black instead of red/black, and extension of yellow color intermediate between *M. cowani* and *M. baroni*).

Distribution. The type locality "East Betsileo" comprises a large area and does not represent a concrete locality. According to a personal communication of A. PEYRIERAS, the species occurs: [1] in forested regions of the highlands SE of Ambatolampy and [2] near Antoetra. MNHN vouchers corroborate the localities [3] Betafo, [4] Itremo and [5] Ambatodradama. See the discussion in the section on distribution of *M. baroni*.

Diagnosis. (1) *Morphology.* A large, slender *Mantella*, SVL 22-29 mm, TTA mostly not reaching the eye but between forelimb insertion and tympanum (only reaching forelimb insertion in a few specimens). Terminal disks of fingers and toes nearly not expanded. Tympanum/eye ratio generally 1/2-3/5. IMT medium-sized (ratio width/length about 2/3). (2) *Dorsal color and pattern.* Head, dorsum and flanks deep black. Rostral and frenal stripes absent. Proximal part of femur and humerus generally red (exceptionally orange or yellow). This color extending on the flanks as small flank blotches, and also present as a broad band on tarsus and foot (sometimes disrupted by black markings). A light spot below the eye sometimes present. All remaining dorsal surface uniformly black. No flashmarks. Iris completely black without light pigment. (3) *Ventral color and pattern.* Black with relatively large, circular whitish-blue markings. Single markings on throat, but no horseshoe marking. Limbs also black with whitish-blue markings, except broad red bands on tibia, tarsus and foot which correspond to those on the dorsal surface.

Mantella haraldmeieri Busse, 1981

Mantella madagascariensis haraldmeieri Busse 1981. *Name-bearing type*: holotype by original designation (BUSSE 1981: 34), ZFMK 25351 male SVL 22.0 mm. *Type locality*: "Fort Dauphin, Sud-Madagascar" according to original description and ZFMK catalogue. – *Other types*: paratypes, ZFMK 21805-7, ZFMK 25352. *Etymology*: named after the German amateur herpetologist Harald Meier who collected the types.

Mantella madagascariensis haraldmeieri: BÖHME & BISCHEFF, 1984, MELER, 1986

Mantella haraldmeieri: PINTAK, 1990; ANDREONE, 1992 (plate IV, fig. 5-6); GLAW & VENCES, 1992a, 1992b (fig. p. 28); ANDREONE, 1993 (fig. 2); BÖHME et al., 1993; HERRMANN, 1993 (fig.); VENCES et al., 1994 (fig. p. 392); GLAW & VENCES, 1994; HENKEL & SCHMIDT, 1995 (fig. p. 53); STANISZWSKI, 1997b (fig.); LARSEN, 1997; PINTAK et al., 1998; VENCES et al., 1998; VENCES & KNIEL, 1998

Other chrysonyms.

Mantella Cowani MOCQUARD, 1902.

Mantella cowani BACHMANN & BLOMMERS-SCHLÖSSER, 1975, BLOMMERS-SCHLÖSSER, 1978, 1979a; BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), 1993 (pl. 19 fig. 103)

Mantella betsileo MEIER, 1980 (part., p. 353, second fig. above), BUSSE, 1981 (part. tab. 1, specimens from Anosyennes).

Identity. – *M. haraldmeieri* has been generally considered as a separate species in recent years (see BÖHME et al., 1993), mainly based on color patterns as (1) a light dorsum sharply bordering the dark flanks, (2) dorsally uniform hindlimb coloration and (3) small, beige flank blotches. MNHN specimens from the Anosy mountains (Chaînes Anosyennes) in southern Madagascar, near the *haraldmeieri* type locality Tolagnaro, were erroneously identified as *Mantella betsileo* by BUSSE (1981). A detailed re-examination of this large series showed that all specimens are clearly to be assigned to *M. haraldmeieri* based on color patterns (1)-(3) as defined above, and further on (4) presence of an unforked sternum (VENCES et al., 1999a), (5) lack of a horseshoe marking, (6) presence of small, rounded light spots on the venter, and (7) ventrally uniformly light colored tibia, tarsus and foot.

In most MNHN specimens, the dorsolateral coloration border is very indistinct or absent; we presume that the dorsal darkening was caused by the formalin fixation to which the specimens most probably have been exposed (see section on *M. nigricans*). In fact, in at least one specimen (MNHN 1973.511), the coloration border is still clearly recognizable.

In several MNHN specimens, the flank blotches are larger than described until present for *M. haraldmeieri* (see fig. 10), indicating the close relationships of *M. haraldmeieri* with the remaining species of the *M. cowani* group.

Comments. (1) *M. haraldmeieri*, according to our personal observations, does not occur in the coastal town Fort Dauphin (Tolagnaro), the type locality, itself, but in nearby rainforest remains near Nahampoana. (2) Probably due to a typing error, BUSSE (1981) did not mention the specimen ZFMK 25353 which has similar collection data as the holotype and paratypes, and was listed in the appendix of BUSSE's (1981) work. Although this specimen was originally catalogued as paratype, it cannot therefore be considered as such (and was not listed in the account of BÖHME & BISCHOFF, 1984).

Material examined. MNHN 1901 232 (Fort Dauphin, envoi de M. ALLAUD, pigments totally faded, identification by size, locality and medium-sized IMT), MNHN 1973 499 (Soavala Ambana, Chaînes Anosyennes), MNHN 1973 500 (Beampingaratra, Nord Bekazaha, alt. 950 m), MNHN 1973 501 (Camp IV⁹), MNHN 1973 502-11 (Camp IV, Ambana), MNHN 1973.512-16 (Camps IV et III bis), MNHN 1973 518-20 (Camps IV et III bis), MNHN 1973 521 7 (Ambana), ZFMK 21805-7 (Fort Dauphin, leg. H. MEIER 1978, paratypes), ZFMK 25351 (Fort Dauphin, leg. H. MEIER 1978, holotype), ZFMK 25352 (Fort Dauphin, leg. H. MEIER 1978, paratype), ZFMK 25353 (Fort Dauphin, leg. H. MEIER 1978), ZFMK 47831-3 (Fort Dauphin, leg. H. MEIER 1988), ZFMK 48181-2 (Fort Dauphin, leg. F. W. HENKEL & R. STIPP 1988), ZFMK 52741-3 (Nahampoana near Fort Dauphin, leg. F. GLAW & M. VENCES 1991, 52741 CS), MRSN A0062 1 2 (Nahampoana, leg. F. ANDRÉONE 14 IV 1990), MRSN A0063 (Nahampoana, leg. R. NINCHERI 14 IV 1990).

Distribution. ZFMK specimens with a reliably known locality were collected in [1*] near Nahampoana. A. PIYRII (personal communication) found the species in [2] Mahatalaha. MNHN vouchers demonstrate that the species is the only *Mantella* so far known in the Anosy mountain chain. Localities are [3] Chaînes Anosyennes; [4] Ambana; [5] Bekazaha; [6] Soavala. See the discussion in the section on distribution of *M. baroni*.

Diagnosis. (1) *Morphology.* A medium sized to large, relatively slender *Mantella*. SVL 21-27 mm. TTA mostly reaching the eye center but in some specimens only the tympanum. Terminal disks of fingers and toes expanded. Tympanum/eye ratio generally 3/5. IMF medium-sized (ratio width/length about 2/3). (2) *Dorsal color and pattern:* Dorsum light brown with three regular dark brown patterns: (a) an either triangular or inversely Y-shaped marking in the shoulder region; (b) a larger, heart-shaped marking at the center of the dorsum; and (c) two spots in the anal region. Flanks dark brown, with a sharp dorsolateral color border. Hindlimbs yellowish-brown with indistinct darker crossbands. Forelimbs cream to beige. Color of limbs extending as mostly rather small flank blotches on the flanks. No flashmarks, postero-dorsal part of femur and knee hollow orange, but without contrast to the surrounding surface. Upper part of iris light. – (3) *Ventral color and pattern:* Forelimb, femur, venter and throat black with many small rounded whitish blue spots. On the throat, these whitish blue spots sometimes are arranged semicircularly along the lip, but they are not fused (not forming a closed horseshoe marking). Foot, tarsus and tibia orange-red. This color sometimes extending onto the distal part of the femur.

***Mantella nigricans* Guibé, 1978**

M[antella] cowani nigricans Guibé, 1978. *Name-bearing type* lectotype, by present designation, MNHN 1973 555, female, SVL 26.3 mm. *Type locality* "massif du Marojezy", according to original description. *Other types* paralectotypes, following present lectotype designation, MNHN 1973 517, MNHN 1973 530-54, and MNHN 1973 556-9. *Etymology* derived from Latin *nigricare* (to darken towards black), referring to the uniformly dark color of the type series which, however, was most probably caused by fixation in formalin.

Mantella madagascariensis nigricans BUSSE, 1981 (part, not MNHN 9594), BLOMMERS-SCHLÖSSER & BLANC, 1991; GLAW & VENCES, 1994 (nomen dubium; p. 412)

Mantella nigricans: VENCES & KNIEL, 1998; STANISZEWSKI, 1998a

Mantella "negrstata" [conditional name]: LARSEN, 1997

Mantella new species. STANISZEWSKI, 1997a (fig. p. 11 and 16).

Mantella sp.: VENCES et al., 1998

Other chresonyms:

Mantella madagascariensis: GLAW & VENCES, 1994 (part.).

Mantella madagascariensis sensu stricto: GLAW & VENCES, 1992a (part.; locality Marojezy)

Identity – The name was erected by GUIBÉ (1978: 84) as the subspecies *Mantella cowani nigricans*. No types were designated. The original description was very short and superficial: "Parfois, au contraire, les taches claires de la racine des membres se réduisent considérablement et finissent par disparaître, le corps et les pattes sont alors uniformément noirs. De tels individus mélaniques se rencontrent en particulier dans le massif du Marojezy, ils correspondent à une sous-espèce: *M. cowani nigricans* n. subsp."

BUSSE (1981) and BLOMMERS-SCHLÖSSER & BLANC (1991: 274) accepted the subspecies in a preliminary way. BUSSE (1981), however, doubted the locality Marojezy and assigned MNHN vouchers from Betafo and Ambatodradama to *nigricans* (these specimens, however, belong to *M. cowani*, see above).

During examination of *Mantella* voucher specimens in the MNHN we noted that all specimens from Marojezy are identified as *Mantella cowani nigricans* in the catalogue. The whole series was catalogued in 1973, while the batrachological MNHN collection was curated

by Jean GUIBÉ. In all these specimens, the light color pattern is largely faded, very probably due to a previous formalin fixation, giving the impression of melanistic specimens. There is little doubt that GUIBÉ's description was based on these specimens, which must therefore be considered as syntypes.

Unfortunately, the syntype series is not homogeneous, it contains some specimens of *M. laevigata* as well as a rather large sample of specimens of a *M. cowani* group species which differs from all other members of the group (see below). In order to reach stability of the name, we here designate one of these specimens as lectotype. This avoids the necessity of creating a new name for the Marojezy populations belonging to the *M. cowani* group.

Mantella nigricans belongs to the *M. cowani* group based on: (1) single click calls (GLAW, personal observation); (2) unforked sternum (VENCES et al., 1999a); (3) lack of horseshoe marking; (4) rounded and isolated ventral spots, (5) lack of a frenal stripe; (6) presence of flank blotches. It differs from all other members of the group by lacking red ventral color on the hindlimbs. Furthermore, it differs from *M. cowani* and *M. baroni* by smaller ventral spots and a different dorsal extension of light (green) color, and from *M. haraldmeieri* by a different dorsal coloration. *M. nigricans* is most similar by dorsal coloration to some specimens of *M. aff. baroni*.

Comment – Of the paralectotypes, only the specimens listed in the *Material examined* section are conspecific with the lectotype; see section of *M. laevigata* for the remaining specimens.

Description of lectotype - MNHN 1973 555, female specimen with nearly mature oocytes. Specimen in good state of preservation with a longitudinal central cut along the venter. Stomach and intestine removed for content analysis and stored separately in small tubes. For measurements, see tab. 2. Body slender, head not broader than body; snout slightly pointed in dorsal, rounded in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye, canthus rostralis weak, straight, loreal region even; tympanum rather indistinct, medium-sized, rounded, its diameter about half of eye diameter; supratympanic fold weakly developed; tongue longish to ovoid, slightly bifid posteriorly, maxillary and vomerine teeth absent, choanae small, rounded. Arms slender, subarticular tubercles single, outer metacarpal tubercle rounded, inner metacarpal tubercle rounded, both rather distinct and of similar size, fingers without webbing; finger length $1 < 2 < 4 < 3$, finger 4 distinctly longer than 2; finger 2 only slightly longer than 1, faintly developed but distinct terminal finger disks. Legs moderately robust, tibiotarsal articulation reaching posterior eye margin, feet with small, slightly elliptical inner and rounded outer metatarsal tubercles; subarticular tubercles single, rounded; toe disks faintly developed but distinct. Foot without webbing. Lateral metatarsalia connected; toe length $1 < 2 < 3 < 5 < 4$, toe 3 distinctly longer than 5. Skin on the upper surface smooth, ventral surface smooth, except for granular thigh patches ("femoral glands") extending from the anus ca. 6 mm distally (max. width 3.6 mm). Color in life unknown, in preservative almost uniformly dark brown, with very little pattern contrast (probably due to formalin fixation). Contours of moderately large light flank blotches faintly recognizable. Venter and ventral side of fore- and hindlimbs, including humerus, fibula, femur, tibia, tarsus and foot, uniformly dark with small rounded light spots. Six spots positioned on the throat along the lip, but not fused to form a horseshoe-marking. No spots in the breast area. No flashmarks.

Material examined MNHN 1973.555 (Marojezy, 600 m, lectotype), MNHN 1973.541 (Marojezy, 300 m, paralectotype), MNHN 1973.530-3, MNHN 1973.550-4, MNHN 1973.556, MNHN 1973.559 (Marojezy, 600 m, paralectotypes); ZFMK 59887-8, ZFMK 59902 (Marojezy Camp 3; leg. F. GLAW & O. RAMILISON II 1995); MRSN A1822 (Tsararano Chain, Camp 2, leg. F. ANDREONE 10.XII 1996), MRSN A1823 1-4, MRSN A1824 1-2, MRSN A1825 (Tsararano Chain, Camp 1, leg. F. ANDREONE XI-XII 1996), MRSN A1829 1-8 (Analabe/Anjanaharibe, Camp 2, leg. F. ANDREONE II 1996), MRSN A1830 (Analabe/Anjanaharibe, near Camp 2 at about 1200 m, leg. F. ANDREONE II 1996)

Distribution. Known from: [1*] the Marojezy massif (North-Eastern region, 300-700 m altitude); [2] Hiaraka (Iaraka) (Masoala peninsula; A. PEYRIERAS, personal communication), [3] Tsararano (700 m altitude), [4] Anjanaharibe (1200 m altitude). See the discussion in the section on distribution of *M. baroni*.

Diagnosis (1) *Morphology*: A medium sized to large, relatively stout *Mantella*. SVL 27-28 mm. TTA reaching the forelimb insertion or the tympanum. Terminal disks of fingers and toes rather largely expanded. Tympanum/eye ratio generally slightly below 3/5. IMT medium-sized (ratio width/length 2/3 to 4/5). - (2) *Dorsal color and pattern*: Relatively variable. Some specimens similar to *M. pulchra* (see below). Flanks black, with a sharp dorsolateral color border. Limbs brown, except humerus and proximal femur; these light green to yellowish green, this color extending as relatively large flank blotches onto the flanks. In other specimens the green color making up the major part of the dorsal surface, including dorsum and flanks (in one specimen the anterior two thirds of the dorsal surface were green) In these cases, however, a strong dorsolateral color border remains on the head. No sharply delimited rostral stripes and no flashmarks. Iris with light pigment in its upper part. (3) *Ventral color and pattern*: Black with small, rounded blue spots. On the throat these spots sometimes arranged semicircularly along the lip, but only exceptionally fusing to form a closed horseshoe marking

Mantella bernhardi group

Mantella bernhardi Vences, Glaw, Peyrieras, Böhm & Busse, 1994

Mantella bernhardi Vences, Glaw, Peyrieras, Böhm & Busse, 1994. *Name bearing type* holotype by original designation (VENCES et al., 1994: 391), ZFMK 57164, male SVL 39.0 mm. *Type locality* "Regenwald nahe Tolongoina, Provinz Fianarantsoa", according to the original description. - *Other types*: none. - *Etymology*: named after the German zoologist Bernhard MEIER

Mantella bernhardi: GLAW & VENCES, 1994, CARISSIMI PRIORI, 1995 (fig. p. 43), STANISZEWSKI, 1996 (plate p. 26), 1997a (fig.), 1997b (fig. p. 21: 40-41: 60 above and middle, probably not fig. p. 37 and 60 below), 1998a (fig.), VENCES et al., 1998

Material examined ZFMK 57164 (S-Mad E-Betsileo [forest near Tolongoina *file* PEYRIERAS], ded. M. VENCES, III 1994, leg. A. PEYRIERAS, holotype), ZFMK 59820-1 (near Tolongoina, leg. PEYRIERAS, ded. F. GLAW IV 1995), ZFMK 62697-8 (locality unknown, CS), ZFMK 62699-707 (locality unknown, TE) MRSN A1964 (Ambohimana next to Tolongoina, leg. F. ANDREONE 20 VII 1995)

Distribution Until now, the species is only known from the type locality: [1] forest near Tolongoina. This locality is corroborated by the observation of F. ANDREONE (personal communication) who, however, found only one single specimen in the dry season.

Table 2 Morphometric measurements of *Mantella* type specimens, and of a reference specimen of *M. milotympanum* (ZFMK 65626). Stat, Status, HT, holotype, PT, paratype, LT, lectotype, PLT, paralectotype, TOT, topotype, M, male, F, female, TT, point that is reached by the tibiotarsal articulation when limbs are addressed along the body. 1, forelimb insertion; 2, nearly to tympanum, 3, tympanum, 4, between tympanum and eye; 5, posterior eye margin, 6, center of eye. See *Materials and methods* section for abbreviations of measurements. Most specimens could not be reliably sexed, generally due to bad state of preservation. Measurements of inner metatarsal tubercle and disk width on third finger were only taken from few equally well fixed specimens. Other lacking measurements are due to damage or bad preservation of the respective specimens.

Collection number	Sex	Stat	SVL	HW	HL	Eye	Tym	Eye-Ns	Ns-St	ForL	Hal	HtL	FoTL	FoI	ToLI	DW3	FW3	IMTL	IMTB	IMIH	TT
<i>Mantella betsileo</i>																					
MNH 1895 278		LT	90	61	82	27	14	19	14	132	60	291	138	87	11	0.37	0.32	0.79			6
MNH 1895 279		PI I	157							104		253									6
<i>Mantella atiemsi</i> (Syn. <i>Mantella betsileo</i>)																					
NMW 20837	F	LT	256	72	92	26	15	21	13	163	71	347	165	114	17	0.7	0.4	0.8	0.4	0.3	5
ZMB 16588	M?	PI I	217	64	94	24	17	20	11	146	64	336	148	97							6
<i>Mantella viridis</i>																					
ZFMK 47900	F	HT	303	89	114	28	20	23	20	177	80	395	188	128	17	0.95	0.68	1.05	0.75		1
<i>Mantella expectata</i>																					
ZFMK 53540	M	HT	234	77	95	29	15	20	15	158	67	348	171	114	11	0.78	0.43	0.85	0.50	0.30	5
ZFMK 53541	F	PT	220	68	86	24	14	18	14	144	63	348	160	109	15	0.73	0.45	0.75	0.53	0.35	6
ZFMK 53542	M	PT	220	68	86	24	14	18	14	144	63	348	160	109	15						6
ZFMK 59095		PT	249	76	100	26	16	16	16	155	74	366	170	114	14	0.70	0.60	0.85	0.58	0.23	6
ZFMK 59096		PT	233	81	98	28	17	20	15	152	70	351	166	111	11	0.73	0.58	0.90	0.63	0.30	5
ZFMK 59097		PT	234	75	94	27	16	17	16	166	64	338	164	107	12						6
ZFMK 59098		PT	236	72	89	28	16	17	12	154	74	345	166	108	14						6
<i>Mantella laevigata</i>																					
TM 10074		HT	225	69	90	24	12	17	16	149	68	332	153	96	18	11	0.4	0.7	0.3	0.3	6
TM 10085		PT	253	73	92	25	12	16	14	173	82	382	176	104	18	11	0.4	1.0	0.4	0.4	5
TM 10086		PI	245	78	103	26	13	22	17	163	74	363	164	105	19	12	0.4	0.9	0.4	0.4	5
TM 10087		PT	244	68	100	26	13	17	19	160	78	368	163	100	20	0.8	0.3	1.0	0.4	0.5	6
TM 10088		PT	204	62	86	24	11	17	11	140	57	316	139	89							6
TM 10090		PT	174	53	78	20	09	15	10	115	46	264	108	69							5
<i>Mantella narom</i>																					
BMNH 1947 2719	M	HT	272	73	109	28	16	22	17	161	71	361	172	111	16						3

Collection number	Sex	Stat	SVL	HW	HL	Eye	Tym	Eye-Ns	Ns-St	ForL	HaL	HiL	FoTL	FoL	ToLI	DW3	FW3	IMTL	IMTB	IMTH	IT
<i>Phrynomantis maculatus</i> (syn. <i>Mantella baroni</i>)																					
MNHN 1991 2845		LT	27.0	7.5	10.9	2.9	1.5	2.0	1.6	17.7	7.7	40.4	18.6	12.4	1.7	0.69	0.46	0.83		0.30	3
MNHN 1991 2846		PI T	26.2	7.6	10.1	3.2	1.5	2.1	1.6	16.9	7.0	39.4	17.2	11.0	1.9	0.57	0.43	0.86		0.44	5
MNHN 1991 2847		PLT	24.9	8.1	9.0	3.1	1.3	2.1	1.6	16.9	7.5	38.4	18.3	11.7	1.6						5
MNHN 6807	F	PLT	28.4	8.0	10.2	2.9	1.9	2.2	1.8	17.2	7.3	39.1	17.5	11.2	1.4	0.61	0.38	1.16		0.51	3
<i>Mantella coxani</i>																					
BMNH 1947 2 7 4		IT	28.2	7.5	10.1	2.8	1.3	1.9	1.6	16.5	7.3	35.8	17.4	11.5	1.6	0.6	0.5	1.0	0.4	0.4	1.2
BMNH 1947 2 7 5		PLT	27.5	7.5	10.3	2.7	1.4	2.0	1.6	16.7	7.1	37.4	18.2	12.3	1.8	0.7	0.6	1.1	0.4	0.3	1.2
<i>Mantella harolaimerei</i>																					
ZFMK 25351	M	HI	22.0	6.8	8.6	2.4	1.4	1.8	1.4	14.4	6.3	34.8	16.0	10.9	1.5	0.85	0.43	0.83	0.38	0.38	6
ZFMK 21805	F	PT	26.8	7.5	10.8	2.6	1.9	2.0	1.5	16.2	6.8	37.2	16.7	10.9	1.7						3
ZIMK 21806	M	PT	23.1	7.0		2.5	1.3	1.8	1.4	13.8	6.0	33.4	15.9	10.6	1.4	0.88	0.53	0.58	0.48	0.25	6
ZFMK 21807	M	PT	21.4	7.2	8.4	2.4	1.4	2.1	1.3	14.0	6.2	33.4	16.4	10.1	1.5						6
ZFMK 25352		PT	22.7	7.0	8.7	2.5	1.4	1.9	1.3	14.5		34.3	16.0	10.3	1.5						6
ZFMK 25353		TOI	24.0	7.0	8.2	2.4	1.4	1.9	1.3	15.7	6.5	35.5	16.3	10.3	1.4						6
<i>Mantella nigricans</i>																					
MNHN 1973 555	F	IT	26.3	7.5	10.4	2.8	1.6	1.9	1.7	17.1	7.3	39.1	18.8	12.3	1.9	1.0	0.5	0.9	0.5	0.5	5
<i>Mantella bernhardi</i>																					
ZIMK 5 164	M	HI	19.0	5.9	8.0	2.2	1.1	1.7	1.2	12.7	5.1	29.1	13.5	8.6	1.4	0.50	0.33	0.65	0.53	0.23	5
<i>Mantella madagascariensis</i>																					
MNHN 1895 276		LT	21.8	6.8	8.4	2.3	1.3	1.9	1.7												
MNHN 1895 277		PI T	17.9			2.2	1.2						13.8	8.9							
<i>Mantella lopesi</i> (syn. <i>Mantella madagascariensis</i>)																					
MNHN 1935 416		PT	28.6	8.4	10.7	3.1	.8	1.9	1.8	16.3	6.8	39.6	18.7	12.6	1.5	0.76	0.60	1.30	0.95	0.85	2
<i>Mantella pulchra</i>																					
BMNH 1947 2 7 20		HI	24.7	7.5	10.3	2.4	1.4	1.9	1.8	15.8	6.6	34.9	16.2	10.9	1.8	0.7	0.5	1.4	0.6	0.6	4
BMNH 1947 2 7 27		TOT	24.7	6.9	9.6	2.5	1.4	1.8	1.6	15.3	6.6	34.8	16.6	10.8	1.9	0.4	0.3	1.3	0.65	0.6	1.2
BMNH 1947 2 7 28		TOT	26.0	7.4	10.7	3.0	1.5	1.8	1.6	15.2	6.0	33.8	16.5	11.0	1.7	0.5	0.4	1.5	0.7	0.3	1.2
BMNH 1947 2 7 29		TOT	24.3	7.1	9.2	2.3	1.7	2.0	1.6	14.5	5.9	32.7	15.6	9.8	1.5	0.7	0.5	1.3	0.5	0.3	3
BMNH 1947 2 7 30		TOT	25.0	7.4	9.9	2.6	1.5	1.8	1.3	15.7	6.1	33.5	15.6	10.3	1.4	0.45	0.35	1.6	0.7	0.5	1-2
BMNH 1947 2 7 31		TOT	21.9	7.2	8.9	2.5	1.4	1.8	1.6	14.3	5.9	31.9	15.5	10.0	1.5	0.5	0.4	1.2	0.7	0.6	3
ZMB 50105		TOT	23.1	6.8	9.1	1.9	1.3	2.1	1.3	13.6	5.2	32.0	16.2								
ZMB 30576		TOT	24.5	7.9	10.0	2.7	1.7	1.8	1.3	15.1	6.7	35.1	17.0	11.7	1.4	0.63	0.43	1.28	0.45	0.43	1
MNHN 1991 2843		TOT	23.9	7.7	10.4	2.8	1.6	2.4	1.7	15.3	6.5	37.2	16.7	11.4	1.5	0.55	0.45	1.50		0.50	3
MNHN 1928 106		TOT	24.8	7.3	10.1	3.2	1.4	1.9	1.8	14.8	6.3	33.2	16.0	10.4	1.4						3

Collection number	Sex	Stat.	SVL	HW	HL	Eye	Iym	Eye- Ns	Ns St	ForL	HaL	HiL	FoTL	FoL	ToL1	DW3	FW3	IMTL	IMTB	IMTH	TT
<i>Mantella aurantaca</i>																					
MNHN 1899 412	M?	LT	21.2	6.0		1.9	1.1				5.5	32.4	15.4	10.2							5
MNHN 1899 413	F	PLT	20.8	5.7		1.9	1.2				5.5	31.0	14.2	9.4							
<i>Mantella aurantaca rubra</i> (syn. <i>Mantella aurantaca</i>)																					
ZFMK 68Ro8	F	LT	24.6	7.8	9.6	2.6	1.6	2.0	1.6	14.1	5.6	31.5	15.2	9.9	1.5	0.6	0.5	0.8	0.6	0.5	3
<i>Mantella crocea</i>																					
ZFMK 45007	F	HT	22.5	6.9	9.4	2.7	1.3	1.6	1.4	13.5	5.6	30.7	14.4	9.7	1.5	0.58	0.40	0.68	0.53	0.40	3
ZFMK 45008		PT	19.3	5.8	8.0	2.1	1.3	1.2	0.9	12.2	5.1	27.6	12.9	7.9	1.4						5
ZFMK 50173		PT	22.0	6.0	8.2	2.0	1.4			13.1	5.4	31.1	14.2	9.6	1.4						3
ZFMK 50174		PT	17.0	5.4	7.7	1.9	1.1	1.4	1.2	11.0	4.4	25.9	12.0	7.7	1.3						5
ZFMK 50175		PT	20.2	6.2	8.7	2.2	1.3	1.8	1.0	1.8	4.9	29.4	13.4	8.8	1.5						5
ZFMK 50176		PT	21.1	6.2	8.3	2.2	1.4	1.6	1.2	12.9	5.4	29.7	14.2	9.0	1.4						3
ZFMK 50177		PT	19.9	5.7	7.8	2.0	1.1	1.6	1.0	13.3	5.6	29.4	14.2	8.9	1.2						5
ZFMK 50178		PT	22.8	6.2	8.2	1.9	1.2	1.9		13.9	5.2	31.4	14.4	9.0	1.7						3
ZFMK 50179		PT	20.7	6.1	7.9	2.1	1.1	1.6	1.2	12.7	5.2	29.7	13.8	9.0	1.3						4
ZFMK 50180		PT	20.4	5.9	8.0	2.2	1.4	1.4	1.1	13.2	5.5	27.5	13.8	8.9	1.3						4
ZFMK 50181		PT	19.5	5.4	7.4	1.8	1.3	1.6		11.8	5.1	29.0	12.8	8.3	1.0						6
ZFMK 50182		PT	17.5	5.3	7.1	1.7	1.2			11.1	4.8	26.3	12.3	9.0	1.2						5
ZFMK 50183		PT	19.3	5.6	7.5	2.2	1.3	1.5	1.0	11.5	4.6	27.0	12.9	8.7	1.2						4
ZFMK 50184		PT	18.5	5.3	7.2	1.8	1.2	1.6	0.9	11.6	5.4	25.8	13.0	8.5	1.5						5
ZFMK 50185		PT	20.3							13.0		29.0	13.0	8.8							
ZFMK 50186		PT	19.6	5.5	8.5	2.0	1.2	1.3	1.2	13.6	4.9	28.4	13.5	9.0	1.5						
ZFMK 50552		PT	20.9	6.0	8.4	2.2	1.3			13.2	5.5	30.7	14.8	9.3	1.5						3
ZFMK 50553		PT	20.8	6.0	7.9	2.2	1.3	1.5	1.2	13.7	6.4	30.7	14.2	8.8	1.4						6
ZFMK 50721		PT	23.0	6.7	8.1	2.5	1.5	1.9	1.2	13.4	5.8	29.8	14.5	9.3	1.6						3
ZFMK 50722		PT	22.4	6.2	7.8	2.0	1.1			13.4	5.6	31.4	15.1	9.8	1.2	0.48	0.33	0.68	0.38	0.70	3
ZFMK 50723		PT	17.4	5.1	6.8	1.8	1.1	1.2	1.1	9.6	4.0	24.0	11.1	7.0	0.9						5
ZFMK 50724		PT	22.9	6.4	9.5	2.4	1.4	1.7	1.2	14.5	5.5	30.9	14.7	9.7	1.7	0.45	0.30	0.55	0.45	0.25	3
ZFMK 50725		PT	20.4	6.1	8.5	2.3	1.2	1.4	1.1	13.3	5.2	29.6	13.8	9.2	1.6						5
<i>Mantella milotympanum</i>																					
ZFMK 65626	M?		22.5	6.4	9.6	2.7	1.7	1.6	1.3	14.4	6.1	31.4	14.7	10.1	1.6	0.5	0.3	0.8	0.5	0.5	3

Diagnosis (1) *Morphology*: The smallest known *Mantella* SVL 19-22 mm, males 19 mm, females 19-22 mm. TTA reaching the posterior eye margin or the eye center. Terminal disks of fingers and toes slightly expanded. (2) *Tympanum/eye ratio* generally 1/2 to 3/5. IMT small (ratio width/length more than 4/5). – (2) *Dorsal color and pattern*. Dorsum and head dark grey or brown. A fine light middorsal line sometimes present. Flanks black. Poorly contrasted dorsolateral color border. No frenal stripe. Humerus yellowish beige, femur bright yellow, this color extending slightly onto the flanks as small flank blotches. Fibula and hands, as well as tibia and feet, brown with generally only one distinct dark crossband, respectively. No flashmarks, but posterodorsal part of femur and knee hollow orange as ventral surface of hindlimb. Iris with light pigment in its upper part. (3) *Ventral color and pattern*: Venter, throat and forelimbs black with few large whitish blue markings which can be irregularly vermiculated, but always with very distinct, largely rounded borders. Throat with a distinct horseshoe marking, often covering most of the throat surface in males, being smaller and sometimes not continuous in females. Tibia and femur orange. Foot and tarsus are also orange, but this color is mostly covered by irregular dark pigment.

Mantella madagascariensis group

Mantella madagascariensis (Grandidier, 1872)

- Dendrobates madagascariensis* Grandidier, 1872. *Name-bearing type* lectotype, by designation of GLAW & VENCES (1994: 403), MNHN 1895 276, sex unknown due to bad preservation, SVL 21.8 mm. *Type locality* Forêt d'Ambalavato, entre Mananjary et Fianarantsoa" according to the original description, given as "forêt d'Ambalavato entre Mananjary et Fianarantsoa" by BLOMMERS-SCHLÖSSER & BLANC (1991). *Other types*: paralectotype, following lectotype designation of GLAW & VENCES (1994), MNHN 1895 277. – *Etymology* named after its geographic origin, Madagascar.
- Mantella madagascariensis* WERNER, 1901, MOCQUARD, 1909, BOULENGER, 1882, BUSSF., 1981 (part.), PINTAK, 1990 (part.), BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), GLAW & VENCES, 1992a (part. see localities), 1994 (part. see localities), HERRMANN, 1993 (fig.), STANISZEWSKI, 1997a (fig. p. 12); LARSEN, 1997 (fig.); VENCES & KNIEL, 1998.
- Mantella m. madagascariensis* MEIER, 1986 (fig. 5).
- Mantella loppetii* ROUX, 1935. *Name-bearing type* holotype as inferred from original description (ROUX, 1935: 441; see comment below), NMB 4849, female (number and sex according to FORCART 1946). *Type locality* "Moroulambo, province de Vatondromy", according to the original description. *Other types* two paratypes according to original description, one corresponding to MNHN 1935 416, and the second specimen probably stored in the La Rochelle Museum (see comment below). *Etymology* named after E. LOPPÉ, former director of the La Rochelle Museum.
- Mantella loppetii* FORCART (1946), BUSSF., 1981 (syn. *madagascariensis*), BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn. *madagascariensis*).
- Mantella "loppetii"* GLAW & VENCES, 1994, STANISZEWSKI, 1997b (fig. p. 57).
- "*Mantella nasuta* sp." [nomen nudum, referring to the "variable" color morph] CLARK, 1994 (fig. p. 10 above and p. 11 above).
- Mantella* sp. [referring to the "variable" color morph] CLARK, 1994 (fig. p. 11 below), VENCES et al., 1994 (fig. p. 391), GLAW & VENCES, 1994 (plates 58-60).
- "*Mantella mystriosa*" [conditional name, referring to the "variable" color morph] BARTLETT, 1995 (fig. p. 18). *Other chrysonyms*
- Mantella pulchra*: GILBÉ, 1964, 1978 (part.).
- Mantella coxani*: WOLPERT & MÜLLER, 1980.
- Mantella coeca*: BARTLETT, 1995 (fig. p. 16 below) [referring to the "variable" color morph].

Identity: Dorsal color patterns of this species are sometimes very similar to *M. baroni*, and single specimens can only be identified by combination of several color characters. The

syntopic occurrence of *M. baroni* and *M. madagascariensis* as recorded by us in Vohiparara, however, demonstrates that both must be regarded as separate species. As far as can be concluded from large series of specimens exported from Madagascar in the pet trade, the pattern is constant at some localities but may be extremely variable elsewhere.

M. madagascariensis was considered as "nomen dubium" by several authors based on the very bad state of preservation of the types and the short and little detailed original description (GUIBE, 1964; DALY et al., 1996). A detailed examination of the lectotype, however, revealed one character which is still recognizable and can be used for a diagnosis. The specimen's dorsal and ventral color has nearly completely faded to uniform brownish. The hindlimbs are separated from the body. The posteroventral part of the femur and the distal part of the tibia, in the knee hollow area, still show some contrasting pattern with an extension corresponding exactly to the flashmarks present in all specimens of the form here attributed to *M. madagascariensis* (see fig. 11). Ventrally, the lectotype shows light color extending onto the distal part of the femur, corresponding to the pattern generally present in the form here attributed to *M. madagascariensis* but not in the otherwise rather similar *M. pulchra* (fig. 12).

Comments. (1) The paralectotype of *M. madagascariensis* is most probably a subadult, but it may also be a *M. bernhardi* and thus not conspecific with the lectotype. (2) Status of two names coined in recent publications to refer to "variable color morphs" must be discussed here. "*Mantella mysteriosa*" was used in quotation marks by BARTLETT (1995). The author states explicitly (p. 20) that this name originated from a pet dealer's list. Diagnosis, type designation and type locality were not given. The name must thus be seen as documentation of the usage of a conditional name in the pet trade, and is not nomenclaturally available. "*Mantella nasuta* sp." was used by CLARK (1994) in the captions of two figures. No unequivocal diagnosis of the specimens figured is possible since neither dorsal pattern of hindlegs nor ventral coloration were documented or described. Further diagnosis, type designation and type locality were not given. No direct reference to the name is to be found in CLARK's (1994) text and key. Two common names, Mimic Mantella and Panther Mantella, are used in the captions of the figures on p. 10-11 to refer to specimens named *Mantella nasuta* sp. Both common names were also included in CLARK's (1994) species list as "*Mantella* sp. A" and "*Mantella* n. sp. 5". The latter two names, on the other hand, are also found in his key. Thus, two forms considered as different species are indirectly keyed as *M. nasuta* sp., and there is no direct diagnosis related to this name, which we consider as a nomen nudum. - (3) *Mantella loppet*, according to the original description (ROUX, 1935), was based on "3 Amphibiens appartenant au genre *Mantella* et qui représentent une espèce nouvelle - M le Docteur Et. Loppé a bien voulu nous autoriser a conserver pour le Musée de Bâle le spécimen-type de l'espèce, tandis que deux autres exemplaires se trouvent au Musée de La Rochelle". Although not explicitly mentioned, this infers the existence of a holotype in the collection of the Basel Museum (NMB 4849 according to FORCART, 1946), and two additional specimens which we consider as paratypes (originally both in the La Rochelle Museum; one later exchanged with the Paris Museum, catalogued as MNHN 1935.416).

Material examined. NMB 4849 (Prov. Vatamandry, Mourouambo, coll. E. PICHON 1930); MNHN 1895 276-7 (Ambalavato, lectotype and paralectotype), MNHN 1931 12 (Moramanga), MNHN 1931 13 (Moramanga?), MNHN 1935 416 (Vatamandry, J. Rot x, "don du DR. LOPPE, Conservateur du Musée de la Rochelle", paratype of *M. loppet*), MNHN 1992 4821-2, MNHN 1993 1440, MNHN 1993 1445

(origine inconnue); ZFMK 14184-207 (Niagarakely; leg. H. MEIER 1972; 14186, 14188, 14196· CS), ZFMK 14209-13 (Niagarakely; leg. H. MEIER 1972); ZFMK 14325-30 (Niagarakely, leg. H. MEIER 1974); ZFMK 14471-5 (Niagarakely; leg. H. MEIER 1973); ZFMK 22107-12 (Niagarakely, leg. H. MEIER 1973); ZFMK 56153-4 (pet trade; ded. F. GLAW XI 1993), ZFMK 60132 (locality unknown, ded. F. GLAW IV, 1995, ZFMK 62740-1 (locality unknown, CS), ZFMK 62732-6, ZFMK 62738-9 (locality unknown, TE), ZFMK 62737 (locality unknown, TE, pattern very similar to *M. baroni*), ZFMK 64138 (Vohiparara, leg. F. GLAW, D. RAKOTOMALALA & F. RANAIVOJAJONA III, 1996; TE).

Distribution. – Type locality is [1] Ambalavato near Ranomafana. Type locality of the junior synonym *M. loppet* is [2] Marolambo (Vatomandry). ZFMK vouchers were collected at [3] Niagarakely. At [4*] Vohiparara (ca. 1000 m altitude, near Ranomafana), we found one specimen syntopic with *M. baroni*. According to A. PEYRIERAS (personal communication), populations of the “variable morph”, here included in *M. madagascariensis*, occur near [5] Beparasy. See the discussion in the section on the distribution of *M. baroni*.

Diagnosis. – (1) *Morphology:* A medium-sized *Mantella*. Compared with *M. baroni*, general body shape rather stout. SVL 20-27 mm, recorded lengths of males 21-22 mm, of females 24-25 mm. TTA rarely reaching the eye center, sometimes the posterior eye margin, mostly the tympanum, and sometimes only the forelimb insertion. Terminal disks of fingers and toes slightly expanded. Tympanum/eye ratio generally 1/2 to 3/5. IMT large (ratio width/length less than 3/5). (2) *Dorsal color and pattern:* Upper head surface, dorsum and flanks black, generally without recognizable dorsolateral color border. Yellowish rostral stripe present. Femur and humerus yellow to green, this color extending as large flank blotches onto the flanks and sometimes onto the dorsum. Distinct orange flashmarks present. Tibia, tarsus and foot orange with or without blackish crossbands and marblings. Iris mostly containing light pigment in its upper part. Rostral stripe often in contact with flank blotch. In specimens of the “variable morph”, yellow color in varying extension can sometimes be present on the dorsum. All intermediate states, from a few yellow spots to a reticulated yellow marbling or a dense yellow speckling, are known. A greenish frenal stripe, often interrupted, can be present as well. Specimens without reliable locality information are known which are nearly uniformly yellow dorsally and ventrally, with only a few blackish spots and marblings. In these specimens, the more distinct yellow surface in the flank blotch area is reminiscent of the typical coloration, but it is not clear whether they really are conspecific with *M. madagascariensis*. (3) *Ventral color and pattern:* Venter, throat and forelimbs black with light markings (mostly whitish-blue, sometimes yellow to green), these being generally rather large, rounded, and situated posteriorly on the venter. Distinct horseshoe marking present, more extended in males. Femur, tibia (except flashmark area), tarsus and foot often uniformly orange, in other specimens with areas of black and yellow (the latter corresponding to yellow color on the dorsal surface). Areas of femoral “glands” often darkly pigmented. In some specimens, femur nearly totally black with blue spots. In “variable” specimens, typical ventral pattern sometimes replaced by a dense yellow marbling.

Mantella pulchra Parker, 1925

Mantella pulchra Parker, 1925. *Name-bearing type* holotype by monotypy, BMNH 1947.2.7.70 (ex 1925.7.2.58), female according to original description SVL 24.7 mm. *Type locality:* “Ants.hanaka” according to original description. *Other types:* none (see comment below). *Etymology:* derived from Latin *pulcher* (beautiful).

Mantella pulchra. GUIBÉ, 1964, 1978 (part.), GLAW & VENCES, 1994; HENKEL & SCHMIDT, 1995 (fig. p. 56), BARTLETT, 1995 (fig. p. 24 above left), VAN TUJL, 1995, CARISSIMI PRIORI, 1995 (fig. p. 43), STANISZEWSKI, 1996 (pl. p. 23), 1997b (fig.), 1998a (fig.), DALY et al., 1996; LARSEN, 1997; VENCES & KNIEL, 1998

Other chrysonomys

Mantella madagascariensis DALY et al., 1984; BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.)

Mantella madagascariensis madagascariensis BUSSE, 1981 (part.).

Mantella sp. cf. *madagascariensis* GARRAFFO et al., 1993

Mantella madagascariensis (colour morph *Mantella "pulchra"*). GLAW & VENCES, 1992a

Mantella cowani pulchra. ANDREONE, 1992, GAVETTI & ANDREONE, 1993 (p. 105).

Mantella cowani. ZIEGENHAGEN, 1981, LE BERRE, 1993 (inner fig. on p. 21).

Mantella sp.: STANISZEWSKI, 1998a (fig.).

Comments. – (1) According to the BMNH catalogue, there were 22 “paratypes” (old numbers BMNH 1925 7.2.59-80), one of which (ex BMNH 1925 7.2.80) was cleared and stained and seemingly not given a new number when the types were re-numbered in 1947. Nine additional specimens were exchanged according to this catalogue. Seven of these were located by us. MNHN 1928.106, MNHN 1991.2843 (ex MNHN 1928.106.A), ZMA 5809-10 (according to VAN TUJL, 1995), ZMB 50105, ZMB 30576, MZUT An 108 (all from Antsihanaka). According to VAN TUJL (1995), “paratype(s)” were also deposited in the MCZ collection. (2) The original description of *M. pulchra* was based on a single specimen (“Type specimen: a female from Antsihanaka”; PARKER, 1925: 394), and contains no mention of other specimens. Although the specimens listed above have similar collecting dates as the holotype, they can therefore not be considered as paratypes. As already stated by GAVETTI & ANDREONE (1993), they must be regarded as topotypes only.

Material examined – BMNH 1947 2 7 20-32 (holotype and paratypes; all from Antsihanaka, coll. or purch. ROSENBERG), MNHN 1928 106, MNHN 1991 2843 (“acquis par échange avec le British Mus. [Nat. History] en 1927”, paratypes), MNHN 1993 1443 (locality unknown), ZFMK 52122-3 (locality unknown; ded. D. KARBE 1991); ZFMK 56155 (locality unknown, ded. F. GLAW XI 1995, CS), ZFMK 62258 (An’Ala bei Andasibe, leg. F. GLAW 3 II 1996), ZFMK 62742-4 (locality unknown, CS), ZFMK 62645-59 (locality unknown; GEJ); ZMB 50105, ZMB 30576 (Antsihanaka, exchanged with BMNH in III 1927, paratypes), MRSN A0059 1-4 (An’Ala [syntopic with *M. baroni*]; leg. F. ANDREONE 4.I 1992 [sacrificed 14 XI 1992]), MRSN A444.1-3 (locality unknown), TM 9893, TM 9897, and possibly the juvenile TM 9901 (Folohy, coll. METHUEN)

Distribution Type locality is [1] Antsihanaka. ANDREONE (1992) and DALY et al. (1996) collected the species near [2*] An’Ala (near Andasibe; ca. 850-1000 m altitude), and A. PEYRIERAS (personal communication) in [3] Andekaleka (Rogez). Further localities within the [4] Mananara reserve (ca. 100-200 m altitude) were published by DALY et al. (1996). Specimens in the TM corroborate the occurrence in [5] Folohy. Exact location of the type locality Antsihanaka is unknown; most probably, it was used in the past for a forested region near Lake Alaotra (see VIETTE, 1991). BLOMMERS-SCHLÖSSER & BLANC (1991, map 4) locate Antsihanaka, probably erroneously, east of Andasibe.

Diagnosis. – (1) **Morphology** A medium-sized *Mantella*. General body shape rather stout. SVL 21-25 mm, recorded length of males 22-23 mm. TTA often reaching the posterior eye margin, sometimes the tympanum or the forelimb insertion. Terminal disks of fingers and toes slightly expanded. Tympanum/eye ratio generally less than 3/5. IMT very large and protruding (ratio width/length less than 1/2). – (2) **Dorsal color and pattern** Dorsum and flanks dark brown to black. On the upper head surface, the dark color of the dorsum gradually fading into light brown. Dorsolateral color border present, indistinct in the inguinal

region, but very distinct in the head and shoulder region. Hand, fibula, foot, tarsus and tibia light brown, with few dark brown crossbands. Humerus and femur yellow to green, in some specimens (locality unknown) blue. This color extending as relatively large flank blotches onto the flanks. Flank blotches delimited by the dorsolateral coloration border and not extending onto the dorsum. Bright red flash marks present. Iris with light pigment in its upper part. (3) *Ventral color and pattern*. Venter, throat, forelimbs and femur dark brown to black with small, generally regularly rounded whitish-blue spots and a distinct horseshoe marking, which in males can cover nearly the complete throat. Tibia with a distinct orange marking, sometimes continued on the knee, distal part of femur and foot. In preservative, this coloration changes, becoming partly bright red and partly white, with a sharp border between both colorations (see also DALY et al., 1996). A similar but less distinct change is also observed in specimens of *M. madagascariensis*.

Mantella aurantiaca group

Mantella aurantiaca Mocquard, 1900

Mantella aurantiaca Mocquard 1900a - *Name-bearing type* lectotype, by present designation MNHN 1899 412, probably a male. SVL 21.2 mm. *Type locality* "une forêt entre Beforona et Moramanga", according to the original description. *Other types* paralectotype, following present lectotype designation, MNHN 1899 413. - *Etymology*: derived from Latin *aurantiacus* (golden).

Mantella aurantiaca MOCQUARD, 1900b, 1909, WERNER, 1901, METHUEN & HEWITT, 1913, GÜBIE, 1964, 1978, ALI DY, 1973, MUDRACK, 1965, 1974, ARNOULT, 1966, MATZ, 1975 (fig.), BALHMANN & BLOMMERS-SCHLOSSER, 1975, BLOMMERS-SCHLOSSER, 1978, 1979a, OOSTVEEN, 1978a-b, MEIER, 1980 (fig. p. 353 above), 1986, BISSÉ, 1981, DALY et al., 1984, 1996, 1997a, UNFRIED, 1987, VAN TOMME, 1988 (fig. 1), AMMER, 1989, SIEGENTHALER, 1989, PINTAK, 1990, OLIVETTI, 1990 (fig.), BLOMMERS-SCHLOSSER & BLANC, 1991, PRESTON-MAFHAM 1991 (fig. p. 79), ANDRIFONE, 1992 (pl. III fig. 1 2), GLAW & VENETS, 1992a, 1994 (part), 1998, ZIMMERMANN, 1992, 1996a-b, ZIMMERMANN & ZIMMERMANN, 1997 (fig. 5, 15 16), 1994, LE BERRE, 1993 (fig. p. 21), GARRATTO et al., 1993, HERRMANN, 1993 (fig.), CLARK, 1994 (fig. p. 7), HAY et al., 1995, BARTLETT, 1995 (fig. p. 18 below left), HENKEL & SCHMIDT, 1995 (fig. p. 49), CARISSIMI PRIORI, 1995 (part fig. p. 41 above and below right), STANISZEWSKI, 1996 (pl. p. 23 and 26), 1997a-b (fig.), 1998a (fig.), 1998b, LARSEN, 1997, PINTAK et al., 1998, VENETS & KNIEP, 1998.

Mantella aurantiaca rubra Staniszeński, 1996 - *Name-bearing type* lectotype, by present designation, ZFMK 68868, female. SVL 24.6 mm. *Type locality*: origin of lectotype unknown, taxon is said to occur in "forests of Anosibe An Ala" according to original description. *Other types*: an unspecified number of (probably lost) paralectotypes. - *Etymology*: derived from Latin *ruber* (red).

Mantella aurantiaca rubra, STANISZEWSKI, 1997b (fig.)

Identity - *Mantella aurantiaca* is one of the early names in the genus, and its status as a distinct species has never been questioned.

Comments (1) The lectotype specimen of *M. aurantiaca* is probably a male, with longitudinal, lateral cuts on both sides on the body, and is in slightly better state of preservation than the paralectotype. The paralectotype is a female in rather poor state of preservation, with a longitudinal cut through the ventral skin. (2) STANISZEWSKI (1996) coined the name *Mantella aurantiaca rubra* for specimens with a red (instead of yellowish-orange) color. His diagnosis, although very short, gives in words one character (color) and should thus be recognized as valid according to the Code. "The type orange form is located in *Pandanus*

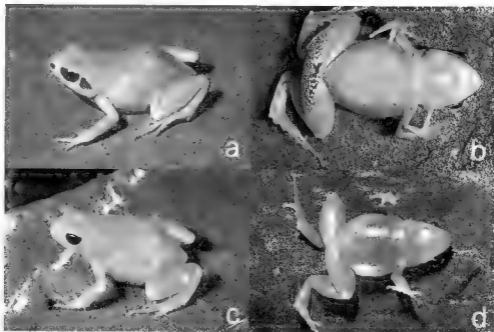


Fig 3 Photographs of *Mantella* species. (a-b) *M. milotympanum*, specimen without locality data (ZFMK 65626), dorsolateral and ventral view, (c-d) *M. aurantiaca*, specimen without locality data, reddish morph (ZFMK 65627), 1997, dorsolateral and ventral view

forests around Andasibe [...] and the deep blood orange form [known as *M. a. rubra*] in the forests of Anosibe An'Ala." No figure was published together with this description, but several color photographs were published later (STANISZEWSKI 1997b, 52-53) by the same author. The assumed type locality Anosibe An'Ala given by STANISZEWSKI (1996) was probably based on GLAW & VENCES (1994), but STANISZEWSKI's captive specimens (including the lectotype described below) almost certainly were obtained through the pet trade without locality; consequently, the taxon *rubra* has currently no type-locality. (3) Regarding the validity of *rubra*, it must be stressed that, according to several authors (e.g. ZIMMERMANN & ZIMMERMANN, 1994, DALY et al., 1996), reddish *aurantiaca* morphs occur at several localities, parapatrically with more orange populations. No evidence supports the status of *rubra* as valid subspecies or species, and no genetic differences were found by allozyme electrophoresis between reddish and orange-colored *aurantiaca* specimens (M. VENCES, personal observation), we consider *rubra* as synonym of *M. aurantiaca*.

Description of the lectotype of Mantella aurantiaca rubra Staniszeński, 1996 ZFMK 68868, adult female with developing oocytes, supplied by M. STANISZEWSKI in 1998 and said to belong to the series on which the original description was based. Specimen in good state of

preservation with a longitudinal cut through right flank. For measurements see tab 2. Body rather stout; head not broader than body; snout rounded in dorsal and lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis weak, straight; loreal region plain; tympanum rather indistinct, medium-sized, rounded, its diameter about half of eye diameter, supratympanic fold weakly developed, tongue ovoid, only very slightly bifid posteriorly; maxillary and vomerine absent, choanae small, rounded. Arms moderately slender, subarticular tubercles single; outer metacarpal tubercle rounded, inner metacarpal tubercle elliptical, both very weakly developed; fingers without webbing; finger length $1 < 2 < 4 < 3$, finger 4 only slightly longer than 2; finger 2 only slightly longer than 1; terminal finger disks nearly not developed. Legs moderately robust; tibiotarsal articulation reaching tympanum; feet with small, rounded inner and outer metatarsal tubercles, subarticular tubercles single, rounded, toe disks nearly not developed. Foot without webbing. Lateral metatarsalia connected; toe length $1 < 2 < 3 < 5 < 4$, toe 3 distinctly longer than 5. Skin on the dorsal and ventral surface smooth. Color in life unknown; in preservative uniformly orange, ventrally translucent orange. Flashmarks visible as yellowish areas. Iris black, pupil whitish (due to fixation).

Material examined - BMNH 1953 1 5 40-41 (Madagascar, pres. G. W. ALLAN), BMNH 1956.1.1.13 (6 specimens NIL) Pérenet District, L. MASON, MNHN 1899 412-3 (lectotype and paralectotype, forest between Beforona and Moramanga), MNHN 1953 137 (Pérenet, forêt), MNHN 1984 117-23 (coll. RAZARIHELISOA), MNHN 1988 7515-25 (pet trade); MNHN 1993 1435-9 (locality unknown), MNHN 1994 1105 10, ZFMK 22113-22 (Pérenet; leg. H. MEIER 1973, 22113, 22115, 22119. CS), ZFMK 56170-83 (locality unknown, ded. F. GLAW XI 1993), ZFMK 62776, ZFMK 62779, ZFMK 62780, ZFMK 62783, ZFMK 62785 (locality unknown, TE); ZFMK 62774, ZFMK 62777 (locality unknown; TE, live coloration orange), ZFMK 62775, ZFMK 62778, ZFMK 62781-2, ZFMK 62784 (locality unknown, TE, live coloration reddish), ZFMK 68868 (locality unknown, lectotype of *M. a. rubra*, ded. M. STANISZEWSKI, 1998).

Additional specimens were not examined in detail, they are here listed according to the catalogue entries: MNHN 1976 235-6, MNHN 1976 240-2 (locality unknown), MNHN 1976 237 9 (forêt de Pérenet [239 tadpoles according to catalogue]), MNHN 1976 243-9 (forêt de Pérenet), ZFMK 8861-70 (Pérenet, leg. H. MEIER 1973); ZFMK 9127-35 (Pérenet, leg. H. MEIER III 1973), ZFMK 13648-9 (Pérenet, leg. H. MEIER 1972), ZFMK 14700 (Pérenet, leg. H. MEIER XI 1974), ZFMK 14331 6 (Pérenet, leg. H. MEIER II 1974), ZFMK 50170-2 (Andasibe [Pérenet], leg. H. MEIER II 1989), ZFMK 51792 (Andasibe [Pérenet], leg. F. W. HENKEL et al. 1988/89), MRSN A0736 1-4 (locality unknown, through the pet trade), MRSN A0060 1-4 (Pérenet [?], leg. F. ANDREONE 24 IV 1990), TM 10047 50, 10053-5, 10057-59 (Ambatoharanana, coll. P. A. Methuen [TM 10051, 10052, 10056 exchanged with MCZ]).

Distribution - Occurrence in Andasibe is often quoted, but most probably the species does not occur in the immediate vicinity of this village, records referring to single introduced specimens. ZIMMERMANN & HETZ (1992) and ZIMMERMANN & ZIMMERMANN (1994) mapped *M. aurantiaca* localities in the area of the Torotorofotsy swamps NW of Andasibe. They found several (more or less isolated) populations, mainly in the northern part of the swamp, one of these consisting mainly of red colored specimens.

Localities are [1*] the Torotorofotsy swamps (including also Antanditra, see BLOMMERS-SCHLOSSER, 1979) and two other localities which are based on a personal communication of A. PYRIERAS uniformly yellow or orange *Mantella* specimens are known from near [2] Beparasy, whereas near [3] Anosibe An'Ala reddish specimens occur. MATHIEU & HAWITT (1913) reported the species from [4] Ambatodradama (Ambatoharanana according to TM catalogue), which, according to their map, is located near Analamazoatra.

Detailed data on the distribution of the species were also included in the unpublished report of BEHRA et al. (1995). These authors, beside delimiting the exact distribution area in the Torotorofotsy area, listed several other localities of uniformly colored *Mantella* in the central part of the Eastern Region. Considering the existence of another uniformly orange species, *M. milotymanum* (see below), specific belonging of these populations is uncertain. Uniformly orange specimens were also observed on the Rantsara plateau between Ihosy and Ivohibe (A. PEYRIERAS, personal communication). This record, however, possibly corresponds to *M. aff. baroni* which occurs on Pic Ivohibe. The locality "Fihierenana valley" (see GLAW & VENCES, 1994) is here referred to *M. milotymanum* (see below). The map shown by UNFRIED (1987), giving the whole of eastern Madagascar as the distribution area of *M. aurantiaca*, must clearly be considered as pure fantasy.

Diagnosis - (1) *Morphology*. A generally rather small and stout *Mantella* SVL generally 19-24 mm, but some females can reach up to 31 mm. TTA reaching the forelimb insertion in large females, the eye center in small specimens, but generally the tympanum or posterior eye margin. Terminal disks of fingers and toes slightly expanded. Tympanum/eye ratio between 1/2 and 3/5. IMT medium sized (ratio width/length slightly less than 3/4). (2) *Dorsal color and pattern*: Uniformly yellow-orange, in some populations red-orange, often with a translucent shade. Bright red flashmarks present. Iris nearly uniformly black, only a little light pigment in its upper part. - (3) *Ventral color and pattern*. Uniform, similar to dorsal surface but generally somewhat lighter, except red flashmark (extended nearly on the whole tibia). Some inner organs visible through the slightly transparent ventral skin.

Mantella crocea Pintak & Bohme, 1990

Mantella crocea Pintak & Böhme, 1990. *Name-bearing type*: holotype by original designation (PINTAK & BOHME, 1990: 59), ZFMK 45007, female, SVL 22.5 mm. *Type locality*: "Andasibe (= Périnet), mittleres Ostmadagaskar", according to original description. *Other types*: paratypes, ZFMK 45008, ZFMK 50173-86, ZFMK 50552-3, ZFMK 50721-5, and 10 (lost) additional paratypes (see comment below). *Etymology*: derived from Latin *croceus* (saffron yellow).

Mantella crocea PINTAK, 1990; BLOMMERS-SCHLÖSSER & BLANC 1991 (p. 274); ZIMMERMANN, 1992; ANDREONE, 1992 (pl. IV fig. 3-4); GLAW & VENCES, 1992a; ZIMMERMANN & ZIMMERMANN, 1992 (fig. 5.23); OTTENS-MANN, 1993; GARRAFFO et al., 1993; HERRMANN, 1993 (fig. 1); ZIMMERMANN & ZIMMERMANN, 1994; GLAW & VENCES, 1994; BARTLETT, 1995 (fig. p. 16 above); HENKEL & SCHMIDT, 1995 (fig. p. 51); ZIMMERMANN, 1996a-b; STANISZEWSKI, 1996 (pl. p. 18 and 23); DALY et al., 1996; STANISZEWSKI, 1997a-b (fig. 1); 1998a (fig. 1); LARSEN, 1997; PINTAK et al., 1998; GLAW & VENCES, 1998.

Other chrysonyms

Mantella viridis: STANISZEWSKI, 1997a (fig. on p. 13 and 17); 1997b (fig. pp. 33, 49, 50); 1998a (fig. 1)

Comments - (1) Since the holotype was supplied by the pet trade, the exact location of the type locality is uncertain. It seems rather probable, however, that it is roughly in the central eastern rainforest region north of Andasibe (formerly Périnet). (2) In the original description (PINTAK & BÖHME, 1990), beside the catalogued specimens, 10 living uncatalogued specimens were designated as paratypes. No specimens of this captive stock were eventually preserved and catalogued; all these additional paratypes must therefore be considered as lost.

Material examined – ZFMK 45007 (Périnet area [?], through pet trade, 1986, holotype), ZFMK 45008 (Périnet area [?], through pet trade, 1986; paratype), ZFMK 50173-86 (Moramanga, leg. H. MEIER II 1989; paratypes); ZFMK 50552-3 (Moramanga, leg. F. W. HENKEL, W. SCHMIDT & V. MÜLLER V 1989; paratypes); ZFMK 50721-3 (Moramanga, leg. H. MEIER 1989; paratypes), ZFMK 50724-5 (Andasibe [Périnet], paratypes), ZFMK 51480-2 (Andasibe [Périnet], leg. O. PRONK II 1990), ZFMK 51738-42 (Périnet, leg. H. ZIMMERMANN 1989), ZFMK 52746 (Andasibe? [Périnet], ded. F. GLAW & M. VENCES 1991, CS), ZFMK 62760-1, ZFMK 62763, ZFMK 62766, ZFMK 62769 (locality unknown, TE); ZFMK 62765, 62767 (locality unknown, TE, live coloration yellow, 62767 CS), ZFMK 62762, ZFMK 62764, ZFMK 62768 (locality unknown, TE, live coloration green); MNHN 1993 1448 (locality unknown); MRSN A0058 (Andasibe [?]; leg. F. ANDREONE 4.I.1992).

Distribution – The type locality (Andasibe) could not be confirmed by recent surveys (see above). Also the Moramanga locality (ZFMK vouchers) seems rather dubious. The only reliable information of which we are aware is included in BETHA et al. (1995), who confirmed the occurrence of the species in the Bakozetra area north of Andasibe (located immediately to the north of the known distribution area of *M. aurantiaca* in the Torotorotsy swamps).

Diagnosis (1) *Morphology*: A small *Mantella*. Small specimens of slender appearance, large specimens rather stout. SVL 17-24 mm, females 23-24 mm. TTA mostly reaching the tympanum or posterior eye margin, rarely the eye center. Terminal disks of fingers and toes expanded. Mean tympanum/eye ratio nearly 3/5. IMT medium sized (ratio width/length slightly more than 2/3). (2) *Dorsal color and pattern*. Head, dorsum and posterior part of flanks yellow, orange or light green, sometimes (mainly in the yellowish specimens) with fine black spots. Sometimes an indistinct dark middorsal line and traces of a diamond marking. Head laterally, and anterior flanks generally black (black pattern can be largely reduced in some specimens), with a sharp dorsolateral color border. Light frenal stripe present, often interrupted in the yellowish specimens. Bright red flashmarks present. Iris with some light pigment in its upper part.

(3) *Ventral color and pattern*. Black with a variable number and extension of grey to bluish-white or yellowish markings, sometimes fusing to form an irregular network. Horseshoe marking present and mostly distinct, but poorly developed in some specimens. Hindlimbs sometimes uniformly orange or reddish ventrally, except the red ventral flashmark extension on the tibia. In other specimens, orange color only present on tibia (except flashmark area); foot, tarsus and femur being black with grey-whitish markings. Pictures of dorsal and ventral coloration of the different morphs were given in GLAW & VENCES (1998).

Mantella milotympanum Staniszewski, 1996

Mantella aurantiaca milotympanum Staniszewski, 1996. *Name-bearing type* lectotype, by present designation, specimen figured on p. 18 of STANISZEWSKI (1996); this specimen was not preserved and must therefore be considered as lost (STANISZEWSKI, personal communication). *Type locality*, the taxon is said to occur in the "Fiherenana Valley in central east Madagascar" according to the original description, but the locality of the lectotype is unknown. *Other types*, an unspecified number of (probably lost) paralectotypes.

Etymology, probably derived from classical Greek *melis* (genitive *melanos*), black (*milo* being a derived spelling which possibly was originally created by pet dealers) and classical Greek *tympanon* (Latin: *as tympanum*), drum (meaning eardrum), referring to the black tympanum color.

Mantella aurantiaca milotympanum; STANISZEWSKI, 1997a (fig.)

Mantella aurantiaca "milotympanum"; STANISZEWSKI 1997b (fig.)

Mantella "milotympanum"; LARSEN, 1997

Other chresonyms

- Mantella aurantiaca* LE BERRE, 1993 (fig. p. 20), GLAW & VENCES, 1994 (part. "black tympanum"),
 CARISSIMI-PRIORI, 1995 (part.; fig. p. 41 below left).
Mantella cf. *aurantiaca*: GLAW & VENCES, 1994 (pl. 52)
Mantella sp. 3 VENCES & KNIEL, 1998.
 "Black-eared mantella": STANISZEWSKI, 1998a.
Mantella sp., Variante 3 GLAW & VENCES, 1998
Mantella sp., Variante 4 GLAW & VENCES, 1998

Identity The name *milotympaanum* was, to our knowledge, first used in a publication by STANISZEWSKI (1996) to name a form of *M. aurantiaca* previously referred to as "black tympanum" variant (GLAW & VENCES, 1994). STANISZEWSKI (in litteris, 1997) had no intention to create a new scientific name, and his paper does not include a formal description nor a type designation. However, it describes distinctive features of the form in a way that must be regarded as a diagnosis:

"I am in no doubt that a mantella currently defined as another subspecies of the golden mantella should be raised to specific status. The black-eared golden mantella (*Mantella aurantiaca milotympaanum*) is so different in appearance and behaviour that it must merit this. [...] The dorsal colour is a slightly drab orange (males brighter than females) while the venter is a greenish yellow (orange yellow in *M. aurantiaca*). This species is overall much slimmer than the golden mantella, the eyes are oblong rather than round and the skin is much more granular. Significant raised veins are apparent on the hind limbs, as its name suggests the eardrum (tympanum) is black as is the nostril region and there is a black line apparent from the eye to the nostril [...]". (STANISZEWSKI, 1996: 24).

According to our observations, the presumed slim habitus is not present in all specimens (especially absent in large females), and the eyes are not of oblong shape (rounded as in other *Mantella*). The presumed "semi-nocturnal behaviour" and "very nervous disposition" were not confirmed by us in our captive group of this species. The same regards the observation of eggs "possessing a yellowish-brown nucleus and measuring only 1 mm in diameter".

Nevertheless, a diagnosis of this form exists (see above), and the name was not used in a conditional way. It must therefore be regarded as nomenclaturally available. Since this form differs from typical *M. aurantiaca* and *M. crocea*, we here consider it as a full species in a preliminary way (see section *Specific status* below).

Comment. The locality information "Fiherenana valley" in the original description almost certainly was based on a personal communication of A. PEYRIERAS as published in GLAW & VENCES (1994). It is not sure that STANISZEWSKI's specimens were collected at this locality.

Lectotype designation We here follow the procedure applied by DL BOIS & OHLER (1997a-b) to stabilize old names for which no type material is preserved in scientific collections but figures were published. The original description (STANISZEWSKI, 1996: 18) includes a color picture which shows all characters currently known as characterizing the form (black pigment on tympanum and around nostril, rather granular skin, dorsal color not of translucent appearance). We designate this figured specimen as lectotype. This specimen (as all specimens kept by M. STANISZEWSKI until the description of *milotympaanum*) was not preserved, and is therefore not available for comparative purposes (STANISZEWSKI, in litteris 1997). A neotype designation is

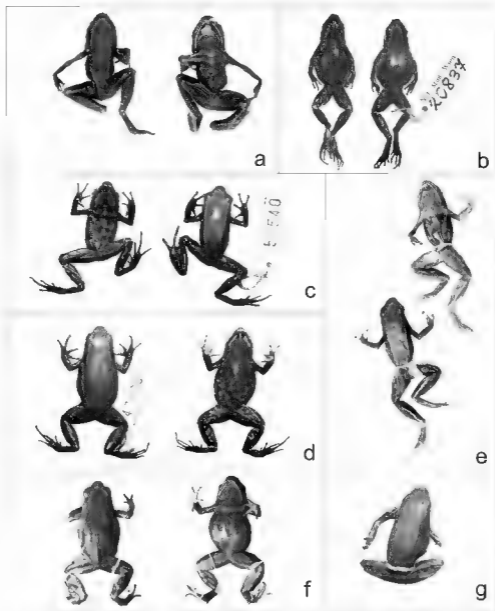
postponed until specimens with reliable collecting data become available. In the following, we describe one reference specimen from the ZFMK collection for comparative purposes.

Description of reference specimen. – Adult male specimen, ZFMK 65626, SVL 22.5 mm. Specimen in excellent state of preservation, with longitudinal cuts along both flanks. For measurements see tab. 2 Body slender; head not broader than body; snout slightly pointed in dorsal, truncated in lateral view, nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis weak, slightly concave, loreal region even; tympanum rather indistinct, medium sized, rounded, its diameter about half of eye diameter, supratympanic fold moderately developed, tongue longish, only very slightly bifid posteriorly; maxillary and vomerine absent; choanae small, rounded. Arms slender; subarticular tubercles single; outer metacarpal tubercle rounded, inner metacarpal tubercle elliptical, both very weakly developed; fingers without webbing; finger length $1 < 2 < 4 < 3$, finger 4 only very slightly longer than 2, finger 2 only slightly longer than 1; terminal finger disks nearly not developed. Legs moderately robust; tibiotarsal articulation reaches tympanum, feet with small, rounded inner and outer metatarsal tubercles; subarticular tubercles single, rounded; toe disks faintly developed. Foot without webbing. Lateral metatarsalia connected; toe length $1 < 2 < 3 < 5 < 4$, toe 3 distinctly longer than 5. Skin on the upper surface smooth, slightly granular on the flanks; ventral surface smooth, except for granular thigh patches (“femoral glands”) extending from the anus ca. 5 mm distally (max. width 3.1 mm). Color in life dorsally, and on flanks and upper surface of fore- and hindlimbs deep orange, except for small black areas around the nostril and covering the tympanum. bright red flashmarks. Ventral side orange except for the dirty blackish “femoral gland” region. After one year in preservative, the orange color has changed to olive greenish. The flashmark areas are yellowish. The ventral side is dirty olive except for the hindlimbs which are yellowish. The “femoral gland” region is dark brown with small whitish spots.

Material examined – ZFMK 62770 (locality unknown; CS), ZFMK 62771 (locality unknown, TE), ZFMK 62772, 65626, 68868 (locality unknown; 62772 TE, live coloration red-orange), ZFMK 62773 (locality unknown, TE, live coloration yellow-orange), MNHN 1992.4823 (locality unknown, identification based on remains of dark pigments on tympanum and around nostril).

Distribution – According to A. PEYRIERAS (personal communication in GLAW & VENCES, 1994) this species occurs in the Fiherenana valley, located about 50 km N Andasibe (not the Fiherenana valley in the South-Western region, near Toliara).

Diagnosis – (1) *Morphology*: Generally, a rather small and stout *Mantella*, although single females can become relatively large. SVL generally 19-23 mm (females exceptionally up to 30 mm, personal observation, specimen not preserved) TTA reaching the tympanum or posterior eye margin. Terminal disks of fingers and toes slightly expanded. Mean tympanum/eye ratio slightly larger than 1/2. IMT rather large (ratio width/length less than 3/5). (2) *Dorsal color and pattern*: Uniformly yellow-orange or red-orange, without translucent shade, and with a black spot covering the tympanum and a little black pigment around the nostril. Bright red flashmarks present. Iris nearly uniformly black, only a little light pigment in its upper part. (3) *Ventral color and pattern*. Uniform, similar to dorsal surface but generally somewhat lighter. Area of “femoral glands” often speckled with blackish. Tibia bright red.



F.g 4 - Ventral and dorsal views of name-bearing types of *Mantella* species. (a) *M. betsileo* (lectotype, MNHN 1895.278), (b) *M. betsileo* (lectotype of *M. attemsi*, NMW 20837); (c) *M. expectata* (holotype, ZFMK 53540), (d) *M. viridis* (holotype, ZFMK 47900), (e) *M. laevigata* (holotype, TM 10074), (f) *M. madagascariensis* (holotype of *M. loppet*, NMB 4849), (g) *M. madagascariensis* (lectotype, MNHN 1895.276). Not to scale



Fig 5 Ventral and dorsal views of name-bearing types of *Mantella* species (a) *M. nigricans* (lectotype, MNHN 1973 555), (b) *M. horaldmeieri* (holotype, ZFMK 25351), (c) *M. baroni* (holotype, BMNH 1947 2 7 19), (d) *M. covani* (lectotype, BMNH 1947 2 7 4), (e) *M. pulchra* (holotype, BMNH 1947 2 7 20), (f) *M. crocea* (holotype, ZFMK 45007), (g) *M. bernhardi* (holotype, ZFMK 57164), (h) *M. aurantiaca* (lectotype, MNHN 1899.412) Not to scale



Fig. 6 – Variation of ventral pattern in species of the *Mantella betsileo* group



Fig 7 Variation of ventral pattern in *Mantella laevigata* and some species of the *M. cowani* group. Diagonally hatched areas represent light coloration which is different from the normal bluish or greyish (exceptionally greenish yellow) spots and markings on the black venter. A further differentiation of the light color was not undertaken, partly because in many preserved specimens the color is largely faded. The diagonally hatched areas thus comprise orange yellowish and light brown areas as well as the flashmark areas of some species which in life are vivid red.

Mantella baroni

MNHN 1933 247

MNHN 1991 1805

MNHN 1936.41

MNHN 1972 775

ZFMK 28870

Mantella cowani

MNHN 1973 528

MNHN 8594

MNHN 1973 529

Mantella crocea

ZFMK 52746

ZFMK 62764

ZFMK 62761

Mantella pulchra

ZFMK 62258

ZFMK 52122

GLAW & VENCES
(1994 fig. 330)***Mantella bernhardi***GLAW & VENCES
(1994 fig. 324)

ZFMK 62702

ZFMK 62705

Mantella madagascariensis

ZFMK 56154

ZFMK 14327

ZFMK 14326

ZFMK 56153

GLAW & VENCES
(1994, fig. 331)

Fig. 8. Variation of ventral pattern in some species of the *Mantella cowani* group, and in species of the *M. madagascariensis* group, *M. bernhardi* group and *M. aurantiaca* group. See also legend of fig. 7

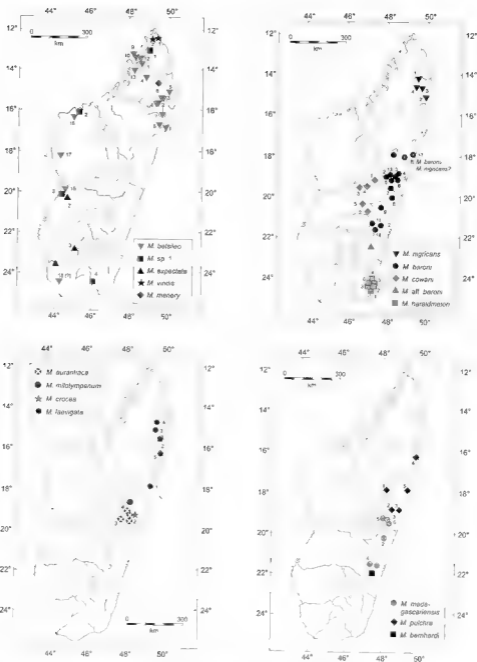


Fig 9 Distribution maps of *Mansiella* species as distinguished in the present paper. Positioning of localities in the maps is only approximate and mainly based on BLOMMERS-SCHLOSSER & BLANC (1991)

KEY TO THE CURRENTLY KNOWN SPECIES OF *Mantella*

The following key should allow identification of all currently known *Mantella* species by their live coloration. Examination of both dorsal and ventral patterns is necessary for a reliable identification. Where useful, we also give morphological, ecological or bioacoustic characters as additional identification aids. A reliable identification of preserved specimens is not always possible, especially in formalin fixed individuals with faded pattern contrast, and in hybrid or rare intermediately colored specimens.

1. Ventral surface of hindlimbs partly or completely orange, yellow and/or red 2
 Ventral surface of hindlimbs black with blue, whitish-blue or greyish markings, without orange or red elements 12
2. Dorsal coloration uniformly green, yellow, orange or reddish, with only rudimentary, dispersed black elements 3
 Dorsally with distinct black or dark brown elements, often covering the largest part of dorsum and/or flanks 6
3. Ventral surface generally black with light markings, at least with some distinct black patterns 4
 Ventral surface uniformly yellow or orange 5
4. Flank blotch area more densely covered by green/yellow than remaining flanks; flashmarks present *M. madagascariensis*, variable morph
 Flank blotch area not more densely covered by green/yellow than remaining flanks; horseshoe marking and flashmarks present *M. crocea*
 Flank blotch area more or less densely covered by green/yellow than remaining flanks; horseshoe marking and flashmarks absent *M. aff. baroni* (Andringitra)
5. Black pigment absent, skin often with a translucent shade *M. aurantiaca*
 Black pigment present on tympanum and around nostril; skin without translucent shade *M. milotympanum*
6. Frenal stripe present 7
 Frenal stripe absent 8
7. Flank blotches present, often integrated in an irregular network pattern of green/yellow and black *M. madagascariensis*, variable morph
 Flank blotches absent, flanks anteriorly black, posteriorly of same color as dorsum *M. crocea*
8. Horseshoe marking present; chirp or trill calls 9
 Horseshoe marking absent; single click calls 11
9. Small species (adult SVL 18-22 mm), IMT small, flank blotches very small, flanks thus nearly uniformly black; dorsum grey, with sharp but little distinct dorsolateral color border *M. bernhardi*

- Larger species (adult SVL 20-27 mm); IMT large; flanks black with large yellow, greenish or blue flank blotches..... 10
10. Dorsum, and especially dorsal head surface, brown, with a distinct dorsolateral color border to the black flanks, femur ventrally generally without red/orange color *M. pulchra*
Dorsum and head surface black (sometimes with green/yellow); femur ventrally generally with red/orange patterns..... *M. madagascariensis*
11. Dorsolateral color border present; flank blotches small, beige; hindlimbs dorsally brown *M. haraldmeieri*
Dorsolateral color border absent; flank blotches medium-sized, generally red; hindlimbs dorsally black with red *M. cowani*
Dorsolateral color border absent; flank blotches large and yellow or greenish; tibia, tarsus and foot dorsally orange with black *M. baroni* and *M. aff. baroni*
12. Frenal stripe and horseshoe marking absent 13
Frenal stripe present; horseshoe marking generally present *M. betsileo* group, 14
- 13 Throat generally uniformly black, without or with very few light markings; flank blotches absent; fingers and toes with largely expanded terminal disks; double click calls, partly arboreal habits..... *M. laevigata*
Throat black with light markings; flank blotches present, fingers and toes with moderately expanded terminal disks; single click calls, terrestrial habits *M. nigricans*
14. Flanks anteriorly black, posteriorly greenish, no dark crossband on tibia... *M. viridis*
Flanks anteriorly black, posteriorly brownish-red *M. sp. 1*
Flanks generally uniformly black or dark brown..... 15
15. Dorsum brownish; dark crossband on tibia present.. *M. betsileo*
Dorsum yellowish, limbs blue to grey, dark crossband on tibia absent .. *M. expectata*
Dorsum yellowish; limbs brown *M. manery*

DISCUSSION

RELIABILITY OF PUBLISHED DATA AND TREATMENT OF "PHANTOM NAMES"

During our survey of literature for the present paper, we became aware of many errors, especially regarding locality data. Furthermore, we noted that during the last years, hobbyists increasingly published unreliable or fantasy data on distribution, behaviour, variation and reproduction of *Mantella* species. With this statement, we do not want to downgrade publications of amateur herpetologists to *Mantella* knowledge in general. Several important contributions were published e.g. by ZIMMERMANN (1992, 1996a-b), MIER (1975, 1980, 1986) and STANISZEWSKI (1998b), among others. However, distributional data such as those of UNFIELD (1987), data on reproduction such as those of LE BERRÉ (1993; *M. laevigata* tadpoles

Table 3. – Phantom names of *Mantella* forms, their identity and current status. Additionally, the following phantom names (with clear mention of their conditional status) were listed by STANISZEWSKI (1998a): *Mantella spezei*, *Mantella crocea calxis*, *Mantella verronique*, *Mantella tulai*, *Mantella mangabe*.

Name	History of name	Taxonomic status	Nomenclatural status
<i>Mantella</i> "mysteriosa" BARTLETT, 1995	not used any more	<i>M. madagascariensis</i> , "variable morph"	conditional name (not available)
<i>Mantella nasuta</i> sp. CLARK, 1994	not used any more	<i>M. madagascariensis</i> , "variable morph"	nomen nudum (not available)
<i>Mantella aurantiaca rubra</i> Staniszewski, 1996	name used in several other hobbyist publications	synonym of <i>Mantella</i> <i>aurantiaca</i>	available name
<i>Mantella aurantiaca</i> <i>milotypanum</i> Staniszewski, 1996	name used in several other hobbyist publications	<i>Mantella</i> <i>milotypanum</i>	available name
" <i>Mantella marojezyi</i> ": STANISZEWSKI, 1996	name used in several other hobbyist publications	<i>Mantella manery</i> , described herein	conditional name (not available)
<i>Mantella</i> "marojezy" LARSEN, 1997	name used in several other hobbyist publications	<i>Mantella manery</i> , described herein	conditional name (not available)
<i>Mantella "negrinata"</i> LARSEN, 1997	name not yet used again	<i>Mantella nigricans</i>	conditional name (not available)

developing within two weeks), habitat data such as those of STANISZEWSKI in his 1997b booklet (e.g. *Mantella crocea* and *M. cowani* occurring in lowland forests), and lists of assumed new species as given in CLARK (1994), lack of any reliable data basis and must largely be seen as inventions of the authors or their informants. Especially the work of Andrew CLARK (1994) must be read with extreme caution in this respect. So, the information of a single specimen collected at high altitude on the Marojezy mountains which belongs to a new species and possibly new genus, quoted by CLARK (1994: 12) as personal communication of R. NUSSBAUM, is false, in fact, no such species was collected, and no such information provided to A. CLARK (NUSSBAUM, in litteris 1997). The major problem is that new scientific names are constantly coined in these papers. New *Mantella* names used without proper description and type designation for the taxon are here referred to as "phantom" names.

As discussed in the corresponding sections and summarized in tab. 3, most phantom names used until now are nomenclaturally not available since they must be regarded as nomina nuda due to the lack of a diagnosis, or as conditional names due to the use of quotation marks. Unfortunately, this does not apply to two of the names coined by STANISZEWSKI (1996), *M. aurantiaca rubra* and *M. milotypanum*, which are stabilized by lectotype designations in the present paper.

As a conclusion, editors of hobbyist journals should not permit their authors usage of new scientific names to name undescribed or undetermined morphs unless the names are accompanied by a formal description and type specimens are deposited in a publicly available scientific collection. Instead of phantom names, authors should be advised to refer to unknown morphs with numbers, letters or localities in quotation marks (e.g. *Mantella* sp. A., *Mantella* sp. 1, *Mantella* sp. "Marojezy").

According to the official information available in December 1998 on the ICZN webpage (www.iczn.org), the fourth edition of the *Code* will include the following requirements for new specific names proposed after 1999 to become available (slightly shortened in the following): (1) the new name must be explicitly indicated as being new (preferably by a term such as "sp. nov."); (2) the description will have to include the explicit fixation for it of a name-bearing type (a holotype or a syntype series); (3) when the name-bearing type of a species-group taxon proposed after 1999 consists of a preserved specimen or specimens, the proposal will be required to include a statement naming the collection(s) in which the name-bearing type is to be found.

Based on our experiences with *Mantella* phantom names, we strongly support these new requirements (as compared to the third *Code* edition currently in force) to valid species descriptions, which will at least avoid "accidental" taxa descriptions in hobbyist journals and pet dealer lists in the near future.

SPECIFIC STATUS

It must be stressed that the taxonomic status of several of the species as defined in the present paper is not yet totally clarified. This concerns *M. maneryi*, for which basic data on morphology and variation are lacking, the species of the *M. aurantiaca* group which appear to be very similar genetically (VENCES et al., 1999b), and *M. pulchra* which may be a subspecies of *M. madagascariensis*. It also concerns *M. aff. baroni*, R. NUSSBAUM (personal communication) collected specimens referable to this form at a locality south of Andringitra, confirming that it occupies a range between those of *M. baroni* and *M. haraldmeieri*. The specific status of these and the remaining taxa of the *M. cowani* group (all apparently distributed allopatrically) must still be confirmed. Specimens with intermediate color patterns are known which possibly are hybrids of *M. baroni* and *M. cowani* (personal observation), and others which may represent intermediates between *M. baroni* and *M. nigricans* (specimens from Zahamena and Folohy; see section on *M. baroni*).

Generally, more detailed data of the species' distribution, variability and genetic differentiation in contact (hybrid?) zones are necessary. Some available data, however, already indicate a substantial amount of differentiation between the taxa mentioned above, so that attribution of specific status to them seems currently the most consistent hypothesis. Our proposal to consider all these forms as distinct species is based (1) on several biological indications, and (2) on practical reasons.

(1) Arguments for the specific distinctness between *M. haraldmeieri*, *M. cowani* and *M. baroni* are (a) the chromosomal differences between *M. baroni* and *M. haraldmeieri* (PINJAK et al., 1998), (b) the morphological differentiation of *M. cowani* (personal observation), and (c)

a relevant genetic differentiation between *M. baroni* and *M. cowani* (VENCES et al., 1999b). The specific status of the closely related, probably allopatric forms *M. madagascariensis* and *M. pulchra* is currently only corroborated by color differences and by a certain genetic differentiation detected by allozyme electrophoresis (VENCES et al., 1999b), but it cannot be excluded that *M. pulchra* is in fact a northern subspecies of *M. madagascariensis*. The very low genetic differentiation between all three species of the *M. aurantiaca* group (VENCES et al., 1999b; determined by allozyme electrophoresis) as well as the rather large color variability of *M. crocea* would support their status as color morphs of one single species. However, (a) the status of *crocea* as separate species was corroborated by chromosomal differences to *aurantiaca* (PINTAK et al., 1998), (b) relevant chromosomal differences were also found between *M. aurantiaca* and *M. milotympanum* (G. ODIERNA, personal communication), and (c) hybridizations in captivity between *M. aurantiaca* and *M. milotympanum* resulted in less vital offspring than simultaneously reared young of *M. aurantiaca* (personal observation).

(2) *Mantella* species are attractive animals which are often kept in captivity and traded in rather large numbers (BEHRA, 1993; GORZULA, 1996). To get an overview of the extent of trade and possibly necessary protection efforts and trade restrictions, it is often useful to have scientific names which can easily and reliably be assigned to forms with a certain, characteristic coloration. For example, *M. aurantiaca* as presently defined has been in the center of conservation efforts and discussions on trade restrictions (e.g. ZIMMERMANN, 1996a), and the inclusion of *M. crocea* and *M. milotympanum* as junior synonyms (respectively their posterior resurrection, since detailed future studies will possibly corroborate their specific distinctness) would cause confusion in conservation organizations and administrations, as for example in CITES authorities. These practical considerations are an additional support for our decision to assign species status to all currently distinguishable *Mantella* forms.

COLOR VARIABILITY

Our results allow for a first time to draw definitive statements on intrapopulational color variability in *Mantella* species. Earlier analyses (e.g. GUIBE, 1964: fig. 2-6) are confusing in this respect since they mixed several populations, belonging to different species, to demonstrate a presumed large variability in single taxa. In the following, we first summarize the current knowledge about intrapopulational color variability, and subsequently the known variability among different populations of the same species. Finally, we discuss deviating color morphs without reliably known localities.

Color and pattern variability within populations

(1) According to our data, dorsal and ventral coloration is rather uniform within populations of *M. baroni*, *M. betsileo*, and also in the one population of *M. aurantiaca* which we observed in the area of the Torotorofotsy swamps. (2) A slight variability is known in *M. laevigata* (Nosy Mangabe population), mainly regarding the posterior extension of the yellow-greenish dorsal color (GLAW & VENCES, 1992b). In *M. huralabremeri*, the extension of flank blotches can vary between individuals (fig. 10). (3) An important variability is observed in the dorsal pattern (extension of yellowish/green color) of *M. nigricans* (Marojezy

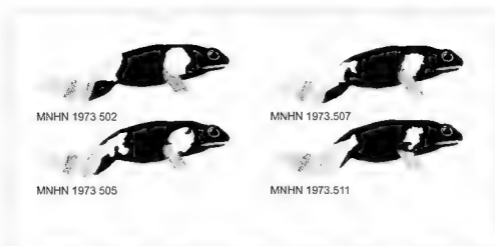


Fig. 10. Size variation of flank blotches in *Mantella haraldmeieri* from the Chaînes Anosyennes. The dorsolateral color border is not sufficiently recognizable in the figured specimens and is therefore not included in the drawings.

population; see fig. 1g-h). In *M.* sp. 1 from Ankarana, the extension of the fiery red flank color is very variable (VENCLIS et al., 1996). Even more extreme variability is found in the dorsal pattern of *M.* aff. *baroni* as it is corroborated by MNHN vouchers which reliably were collected at the same locality. (4) Too little is known for reliable statements on intrapopulation variation of the remaining species.

Color and pattern variability among populations

(1) According to the existing data, differences are rather low between populations of *M. baroni* (see also DALY et al., 1996 and ANDREONE, 1993), except for the deviating specimens from the localities Folohy and Zahamena at the probable northern distribution edge. Similarly, no differences are known between *M. laevigata* populations. (2) Slight differences are known in *M. betsileo*, the Kirindy population differs from the east coast and Sambirano populations by reddish brown crossbands on the hindlegs, and a lighter leg color (VENCLIS et al., 1996). - (3) Too few data are available on most other species; a high variability among populations may be found in the *M. aurantiaca* group when more extensive fieldwork is carried out on these species. The same is true for *M. madagascariensis* (see below), in which the observed high variability may also be due to intrapopulation variation.

Color and pattern variability in specimens without reliable locality information

(1) In some cases, deviating colorations have been observed in single specimens. One *M. laevigata* specimen from the pet trade had brown instead of black legs (GLAW et al., 1998).

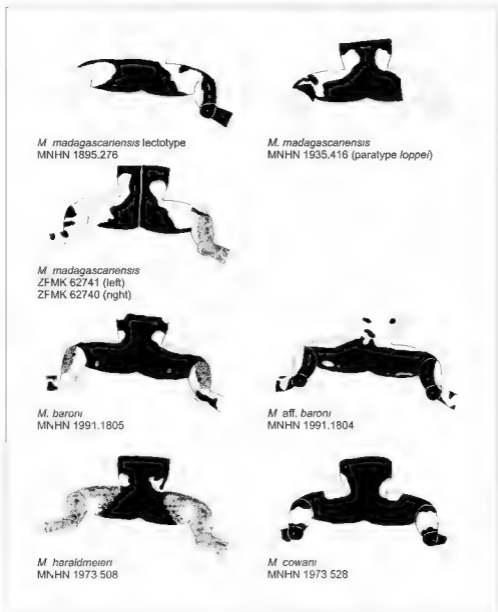


Fig. 11 Pattern on posterodorsal femur and knee hollow in the lectotype of *Mantella madagascariensis* and in several *Mantella* species which occur in the Eastern, Central and South-Eastern Regions of Madagascar. The pattern of the lectotype clearly corresponds best to that of the paratype of *M. loppei* (to be considered as junior synonym of *M. madagascariensis*) and to other specimens here considered as *M. madagascariensis*. The dotted line on the femur of the ZFMK specimens marks the (sharp) color border between yellow (above) and orange (below) which is only visible in life or shortly after preservation. Regarding dorsolateral color border of *M. haraldmeieri*, see caption of fig. 10.



M. madagascariensis lectotype
MNHN 1895 276



M. madagascariensis
MNHN 1935 416



M. baroni
MNHN 1991.1805



M. aff. baroni
MNHN 1991 1804



M. cowani
MNHN 1973 528



M. haraldmeieri
MNHN 1973 508



M. bernhardi
ZFMK 57164 (holotype)

Fig 12 Ventral pattern on femur and tibia in the lectotype of *Mantella madagascariensis* and in several *Mantella* species which occur in the Eastern, Central and South-Eastern Regions of Madagascar. The pattern of the lectotype clearly corresponds best to that of the paratype of *M. loqueti* (MNHN 1935 4.6), but not to *M. bernhardi* which has a ventrally uniformly light femur.

(2) Specimens with intermediate coloration (possibly in some cases due to hybridization) are known between *M. baroni* and *M. cowani* (personal observation), and between *M. nigricans* and *M. baroni* (specimens from Folohy and Zahamena). Also, *M. crocea* specimens are known which have a nearly uniform (greenish or yellowish) dorsal color, with only remains of a dark ventral pattern, and thus appear very similar to *M. milotympanum* (GLAW & VENCES, 1998).

(3) DALY et al. (1996) were right in stating that information based on specimens from the pet trade should be seen with caution, but large series of specimens seen in the cages of the same dealer at the same time (personal observation) allow, in our opinion, the conclusion of important variability (dorsally and ventrally) in *M. madagascariensis*. Whether this variability is between different uniform populations, or within single variable populations, cannot be decided at the current state.

Causes of variation

As in dendrobatids (MYERS & DALY, 1983), the evolutionary mechanisms causing the observed intrapopulational variation (contrasting with the uniformity in other populations) in some species are not yet understood. Considering the presence of skin alkaloids in *Mantella* (DALY et al., 1996), their coloration can be seen as largely aposematic. It is thus possibly subject to strong predatory selective pressures, and phenomena of Müllerian mimicry, which seem to be exceptional among anurans (DUELLMAN & TRUEB, 1985), may also be involved.

SYNTOPY

According to the data presented herein, the following reliable cases of syntopic occurrence of different *Mantella* species are known (the possible syntopic occurrence of *M. expectata*, *M. betsileo* and *M. sp. 1* near Morondava needs confirmation): (1) *M. baroni*/*M. pulchra* (An'Ala; ANDREONE, 1993, DALY et al., 1996; personal observation), (2) *M. baroni*/*M. madagascariensis* (Vohiparara, personal observation, Niagarakely, based on ZFMK vouchers); (3) *M. nigricans*/*M. laevigata* (Marojezy, Camp 3, personal observation); (4) *M. laevigata*/*M. manery* (Marojezy, Camp 1; personal observation); (5) *M. laevigata*/*M. betsileo* (Mananara, DALY et al., 1996); (6) *M. betsileo*/*M. pulchra* (Mananara, DALY et al., 1996).

It is remarkable that these few cases all refer to species of different species groups occurring syntopically. On the other hand, in several groups the species appear to be allopatrically distributed. This is most distinct in the *M. cowani* group (see fig. 9). Also the two taxa of the *M. madagascariensis* group seem to be distributed in an allopatric north-south pattern, whereas the species of the *M. aurantia* group are probably distributed parapatrically in swamp forest and rain forest areas in the east. Only in the *M. betsileo* group are the areas of different forms (*M. betsileo*, *M. sp. 1*, *M. expectata*) known to overlap. It is not known whether in these overlap areas the distribution patterns are at least locally of close syntopy or always of parapatry.

Table 4. – Regional endemism in *Mantella* species.

Region	Number of species	Number of endemic species	Endemism
South-West	2-3	0	0 %
West	2-3	0	0 %
South-East	1	1	100 %
East	10	8	80 %
Center	1	1	100 %
North-East	4	2	50 %
Northern Center	1	0	0 %
North	2	1	50 %
Sambirano (N.-W.)	1	0	0 %

BIOGEOGRAPHY

The almost complete re-examination of the historical voucher specimens and review of recent field data in the present paper enabled us to present updated distribution maps. The resulting distribution patterns of many species, especially those of the *M. cowani* group, are very different from those presented by BUSSE (1981) and BLOMMERS-SCHLÖSSER & BLANC (1991).

All *Mantella* species are exclusively distributed on Madagascar and its adjacent islets (Nosy Be, Nosy Komba, Nosy Boraha, Nosy Mangabe). Records of *Mantella* species on La Réunion island (THOMINOT, 1889; GUIBÉ, 1964) or the Seychelles (STANISZEWSKI, 1997b) are not corroborated by reliable voucher specimens, and must be considered as wrong.

Most *Mantella* species inhabit areas of tropical rainforest but at least three species (*M. expectata*, *M. besileo*, *M. sp. 1*) are known from arid regions in western Madagascar. Although there are no reliable altitude data for most localities, it can be stated that they are mostly in-between sea level and ca. 1000 m altitude. Only *M. cowani* is known to occur at much higher altitudes (Ambatodradama: 2000 m).

According to ANGEL (1942), as modified by BRYGOO (1971), GLAW & VENCES (1994) and RAXWORTHY & NUSSBAUM (1995), Madagascar was herpetogeographically divided into the Eastern Domain and the Western Domain, each consisting of various regions. The Western Domain contains the Western and South-Western Regions, the Eastern Domain contains the South-Eastern, Eastern, Southern Central, Central, North-Eastern, Northern Central, Northern and Sambirano (North-Western) Regions. Here we follow the delimitation of regions in the map 3 of GLAW & VENCES (1994).

In contrast to other terrestrial vertebrate groups as the dwarf chameleons of the genus *Brookesia* (see RAXWORTHY & NUSSBAUM, 1995), the northern biogeographic regions (North-West, North, Northern Center, North-East) do not appear to be a diversity center for *Mantella* (as compared to the Eastern Region, see tab. 4). All six species groups defined herein have representatives in the Eastern Region, whereas only three (*M. laevis* group, *M. betsileo* group, *M. cowani* group) have representatives in one of the northern regions. The Eastern Region harbours at least 10 *Mantella* species, whereas only between one and four species are known from each of the northern regions (six species altogether). None of the species groups is endemic to the northern regions, whereas three species groups are endemic to the East. Three species (*M. viridis*, *M. manery*, *M. nigricans*) are endemic to the northern regions, whereas eight species are endemic to the East.

However, these counts may draw a biased picture since many species of the East show in fact a very low genetic differentiation (VENCES et al., 1999b), and some species complexes may better be seen as single units for biogeographic comparisons. Counting the *M. aurantiaca* group and the *M. madagascariensis* group as single units, and seeing *M. aff. baroni* as closely related to *M. baroni*, reduces the importance of the Eastern Region as center of diversity and, especially, endemism of *Mantella*. It also is interesting that the northern regions are mainly inhabited by species which are considered as relatively basal within the genus (PINTAK et al., 1998; VENCES et al., 1999a-b). *M. laevis* and the *M. betsileo* group. Also *M. nigricans*, due to the lack of reddish ventral hindleg color, can be seen as the most basal representative of the *M. cowani* group.

CONSERVATION

Among the anurans of Madagascar, and beside the tomato frogs (*Dyscophus antongili* and *D. gurneyi*), *Mantella* is certainly the group most attractive to the pet trade. According to BEHRA (1993), a total of 10597 *Mantella* specimens were legally exported from Madagascar in the first half of 1990. *Mantella* species have been subject of discussions on trade restrictions and CITES inclusion. During several years, *Mantella aurantiaca* was the only species included in the CITES regulation (appendix 2) due to its assumed restricted distribution and vulnerability. In 1997, inclusion of several other species (*M. haraldmeieri*, *M. bernhardi*, *M. cowani* and *M. viridis*) was discussed. Also, *Mantella* have been used as key species for the justification of expansion or implementation of natural reserves (e.g. ZIMMERMANN, 1996).

The basis of all these discussions were the published distributional data and species definitions, as well as some unpublished reports. For statements on vulnerability by excessive collecting or habitat destruction, and identification of conservation priorities, a comparative assessment of the status of all *Mantella* species is necessary. In the following we analyze five different factors which may influence the status of *Mantella* species.

(1) *Geographical distribution of the species* – We estimated the extent of the distribution area and the density by which it is populated by a certain species by the total number of localities known and the largest distance in kilometers between two locality records attributed to the species. Species can be classified as follows: (a) common species with a large distribution

area (≥ 10 localities, and > 400 km distance between the most distant localities): *M. betsileo*, *M. baroni*, (b) more localized species with a large distribution area (≤ 5 localities, > 400 km distance): *M. sp. 1*, (c) relatively common species with a moderate distribution area (> 5 localities, 100-400 km distance): *M. laevigata*, *M. madagascariensis*, *M. cowani*, (d) more localized species with a moderate distribution area (< 5 localities, 100-400 km distance): *M. expectata*, *M. pulchra*, (e) species with a small distribution area (≥ 3 localities, 50-100 km distance): *M. nigricans*, *M. haraldmeieri*, *M. aurantiaca*; (f) localized species which are only known from one or two localities (distance < 50 km): *M. manery*, *M. viridis*, *M. bernhardi*, *M. crocea*, *M. milotympanum*.

(2) *Number of nature reserves and protected areas in which a species is known to occur* – At present, this is known to apply to the following species and localities: *M. betsileo*, Tsaratanana, Mananara, Masoala, Lokobe, Manongarivo, Tsingy de Bemaraha, *M. sp. 1*, Ankarana; *M. expectata*, Isalo; *M. manery*, Marojezy; *M. laevigata*, Mananara, Nosy Mangabe, Anjanaharibe-Sud, Marojezy, *M. baroni*, Analamazoatra, Mantady, Ranomafana, probably Zahamena; *M. aff. baroni*, Ivohibe; *M. nigricans*, Anjanaharibe-Sud, Marojezy, probably Masoala, *M. haraldmeieri*, possibly Andohahela; *M. madagascariensis*, Ranomafana; *M. pulchra*, Mananara, *M. aurantiaca*, not yet known from any protected area (would occur within the limits of Analamazoatra if this reserve was expanded as suggested by ZIMMERMANN, 1996b).

(3) *Restriction of the species to primary (forest) habitat* – Field data are lacking or insufficient for most *Mantella* voucher specimens examined in the present study. However, some authors give reliable habitat data of *Mantella* species, which are here combined with our personal observations. Species which are until now only found in primary rainforest are *Mantella laevigata* (localities Nosy Mangabe, Marojezy, personal observation, Anjanaharibe, Tsararano: personal communication of F. ANDREONE), *M. baroni* (several localities; ANDREONE, 1993, DALY et al., 1996, personal observation), *M. haraldmeieri* (pristine and degraded primary forest near Nahampoana, personal observation), *M. nigricans* (Marojezy, Tsararano, Anjanaharibe, personal communication of F. ANDREONE and personal observation), *M. manery* (personal observation), *M. madagascariensis* (Ranomafana; personal observation), *M. pulchra* (several localities, ANDREONE, 1993, DALY et al., 1996, personal observation), *M. aurantiaca* (swamp forest near Andasibe; personal observation, ZIMMERMANN et al., 1990), *M. crocea* (swamp forest; DALY et al., 1996), and *M. bernhardi* (a single specimen found in degraded primary forest rests near rice fields; personal communication of F. ANDREONE). Species known from more arid forest are *M. viridis* (personal observation at Montagne des Français, see also DALY et al., 1996), *M. expectata* (Isalo, DALY et al., 1996) and *M. sp. 1* (Ankarana; personal communication of J. KOHLER). Only *M. betsileo* is known to occur regularly outside primary habitats (personal observation on Nosy Be, Nosy Komba, Nosy Boraha and near Maroantsetra). For the remaining species, no reliable field observations are available to us, however, it is to be expected that *M. milotympanum* is restricted, as *M. aurantiaca*, to swamp forests.

(4) *Extent of trade of the species* – Although trade statistics do exist, a comparison of numbers of traded specimens between species is not possible due to taxonomic confusion in the past. In many cases, it is not possible to state which species actually was traded under a certain name. Therefore we prefer to summarize our subjective impressions made between

Table 5. – Conservation status and trade of *Mantella* species. For each species we give: the number of known localities, the maximum distance between the most distant known localities (± 20 km) measured on a 1:2,000,000 map (*Carte routière, Foiben Taosarintann'I Madagasikara* [Institut National de Géodésie et Cartographie, Madagascar]) as very rough estimate of the distribution area; the number of nature reserves in which the species is known to occur; its known restriction to primary forest habitat (+ restricted to primary forest; - not restricted to primary forest); the frequency in which we have seen it in trade (only our subjective impressions between 1990-1997: - not exported in relevant numbers, + exported, ++ often exported); and the potential attractiveness for hobbyists and the pet trade (+ not very attractive, ++ attractive, +++ very attractive) Status is coded as follows: OK, not threatened, CT, commercially threatened (potential danger of overcollecting exists at least locally); R, rare; K, insufficiently known, I, indeterminate; V, vulnerable. Research needs are coded as follows: 1, distribution; 2, taxonomic status and validity; 3, variation, 4, habitat

<i>Mantella</i> species	Number of localities	Maximum locality distance	Number of reserves	Restriction to primary forest	Traded	Attractiveness	Status	Research needs
<i>M. betsileo</i>	17 (18)	840 (1220) km	6	-	+	+	OK	-
<i>M. sp. 1</i>	5	1260 km	1	(-)	-	+	K	2, 3
<i>M. viridis</i>	2	< 20 km	0	(-)	++	++	R	1
<i>M. expectata</i>	3	340 km	1	(-)	+	+++	R	1, 4
<i>M. manery</i>	1	0 km	1	+	-	++	K	1, 2, 3, 4
<i>M. laevigata</i>	5	360 km	4	+	+	+++	CT	-
<i>M. nigricans</i>	4	80 km	3	+	-	++	CT	2
<i>M. haraldmeieri</i>	6	50 km	1?	+	-	+	R	2
<i>M. baroni</i>	16 (18)	420 km	3 (4)	+	++	+++	CT	-
<i>M. aff. baroni</i>	1	0 km	1	?	-	+++	K	1, 2, 3, 4
<i>M. cowani</i>	5	160 km	0	?	++	+++	R	1, 2, 3, 4
<i>M. bernhardi</i>	1	0 km	0	+?	+	+	V	1, 4
<i>M. pulchra</i>	5	320 km	1	+	+	++	CT	2, 3
<i>M. madagascariensis</i>	5	260 km	1	+	++	+++	CT	3, 4
<i>M. crocea</i>	1?	0 km	0	+?	+	++	I	1, 2, 3, 4
<i>M. aurantiaca</i>	4	60 km	0	+	++	+++	V	1, 3
<i>M. milotympanum</i>	1	0 km	0	?	+	+++	I	1, 2, 3, 4

1990 and 1997. In these years, we monitored several times the exhibitions of specialized pet dealers in Germany as well as in Madagascar, and thus got some indications on extent of trade of certain species which are summarized in tab. 5. Our impressions are relatively well in accordance with the data of GÖRZULA (1996), who reported the incidence of *Mantella* species among a sample of 69 European hobbyists: *M. aurantiaca*, 15.9%, *M. madagascariensis* (probably partly referring to *M. baroni*) and *M. crocea*, 14.5% each, *M. cowani* (possibly also largely referring to *M. baroni* or *M. madagascariensis*), 11.6%; *M. pulchra* 4.4%; *M. viridis*, 2.9%; *M. betsileo* and *M. haraldmeieri*, 1.5%. Also the list of BEHRA (1993) of *Mantella* exported in 1990 from Madagascar does not contradict our observations. *M. aurantiaca*,

30.5 %; *M. viridis*, 14 %; *M. betsileo*, 3 %; *M. cowani* (probably largely referring to *M. baroni*), 29 %, undetermined species, 23 %.

(5) *Potential subjective attractiveness to hobbyists*, estimated by amount of colorful pattern and interest of breeding biology (in *M. laevigata*).

To summarize these data, we tried to assign status categories to *Mantella* species. We followed categories used in the European CITES regulations (ANONYMOUS, 1996), except the category CT ("commercially threatened") which we used in a modified way as specified below, and the abbreviation OK which we used for non-threatened species.

(1) *OK (not threatened)* – Not threatened at present is *M. betsileo*, which has a low attractiveness, a very large distribution area, and also occurs outside primary forest

(2) *K (insufficiently known)*. – *M. manery* and *M. aff. baroni* are expected to belong to one of the categories below (probably R), but basic information is lacking. *M. sp. 1* does not seem to be threatened at the moment due to its low attractiveness and apparently large distribution area; this species, however, may be more locally restricted than *M. betsileo*, and more dependent on a threatened habitat type (dry forest). Also in this case, more data are needed

(3) *CT (commercially threatened)*. – This category is here used for species which may be locally and potentially affected by overcollecting due to their high attractiveness, but which are not yet threatened in their whole distribution area. In this category, we include *M. laevigata*, *M. nigricans*, *M. baroni*, *M. pulchra* and *M. madagascariensis*

(4) *R (rare)* – Species with restricted distribution areas which are not yet vulnerable or endangered, but are at risk. In this category, we include *M. viridis*, *M. expectata* and *M. cowani*.

(5) *V (vulnerable)* – Species likely to become soon endangered by extinction if causal factors continue operating. At present, we only include *M. aurantiaca* and *M. bernhardi* in this category

(6) *I (indeterminate)* – Species known to be endangered, vulnerable or rare, but for which there is not enough information to say which of the categories is appropriate. We include *M. crocea* and *M. milotympanum* in this category

We do not yet assign any known *Mantella* species to the "endangered" category (species facing a very high risk of extinction in the wild in the near future), but some species might move to this category within the next ten years.

Considering the lack of basic knowledge on distribution, variation, and taxonomic status of many *Mantella* species, and the vulnerability of several of them (see tab. 5), we propose the following research priorities:

(1) Clarification of taxonomy and distribution of the species of the *M. aurantiaca* group, by detailed mapping of color morph occurrence and genetic studies along hybrid zones. Single voucher specimens from each recorded locality should be deposited in publicly available scientific collections.

(2) Habitat descriptions and mapping of *M. expectata*, *M. cowani* and *M. bernhardi*

- (3) Clarification of the taxonomic status of *M. aff. baroni* and of *M. baroni* from the Zahamena area.
- (4) Studies on variability in the *M. madagascariensis* group (status of *M. pulchra*, identity of the "variable morph(s)" of *M. madagascariensis*).
- (5) Formal description and naming of *M. sp. 1*.
- (6) Comparative studies on the microhabitat and ecology of all *Mantella* species.

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